

Ecology of the Iguanid Lizard *Callisaurus draconoides*

ERIC R. PIANKA AND WILLIAM S. PARKER

Various aspects of the life history of *Callisaurus* are described and discussed, including: movements, microhabitat, foraging behavior, diet, size, growth, age, population structure, reproduction, sexual dimorphism, sex ratio, abundance, thermoregulation, time of activity, tail loss and predation, and leg length.

Callisaurus hatchlings emerge from mid-July through November and grow rapidly, with most individuals attaining minimum adult size at ages of less than a year. Mean distance between captures was 20.3 m in seven immatures and 31.9 m in six adults. Mean growth rate of nine first-year lizards was 6.5 mm per month. One or more clutches of two to eight eggs are laid annually (mean of 73 clutches: 4.42). Oviducal eggs, and presumably egg deposition as well, occur from early June through at least late August. Males have enlarged testes from April through mid-August on southern areas, whereas on northern areas testes are reduced in size during late July and August, suggesting a shorter breeding season in the north. Clutch size is not correlated with female snout-vent length or with any of several measures of precipitation. Estimates of abundance vary from about .02 to 1.75 lizards per hectare, but are not correlated with the percentage of open ground, or with any of several precipitation statistics. There are latitudinal shifts in diet and percentage of females with broken and regenerated tails, and it is likely that the available prey and the level of predation differ within the geographic range. The frequency of broken tails increases with size, perhaps reflecting increased numbers of contacts with predators as the lizards age.

Both the forelegs and the hindlegs of *Callisaurus*, expressed as percentages of snout-vent length, are significantly longer than the same measurements on eight other species of North American desert iguanids. Hindleg length is correlated with the frequency of use of open spaces in North American flatland desert lizards. Various aspects of the ecology of *Callisaurus* are briefly compared with those of some related and/or ecologically similar species of lizards.

INTRODUCTION

ALTHOUGH often uncommon, the zebra-tailed lizard, *Callisaurus draconoides*, is a widespread and conspicuous desert lizard in western North America. No one has studied its ecology in any detail, however, and what is known about this monotypic genus is scattered through numerous publications. Here we consolidate the diffuse literature on *Callisaurus* and present some new information on its ecology from our own studies. Aspects of its ecology are briefly compared with those of related North American species in the genera *Holbrookia* and *Uma*, as well as with the ecologies of some independently evolved but ecologically similar species in the Australian agamid genus *Amphibolurus*.

The sketchy knowledge of the life history and habits of *Callisaurus* in the early part of this century was summarized by Van Denburgh (1922). Pack (1923), Knowlton and Thomas (1934), Knowlton and Smith (1935) and Knowlton (1938) examined its diet. Mosauer (1932, 1936) commented on the enlarged toe lamellae of the sand-dwelling Baja California race *Callisaurus d. crinatus*, and on the upper lethal body temperature of *Callisaurus d. gabbi*. Atsatt (1939), who experimented with temperature dependent color changes, showed that the albedo pale color phase is assumed only by animals with high body temperatures. Klauber (1939), Johnson et al. (1948), Gates (1957) and Miller and Stebbins (1964) made miscellaneous observations on its natural history. Activities of

TABLE 1. LOCATIONS OF THE STUDY AREAS AND DATES THEY WERE VISITED.

Area	Latitude	Longitude	Location	Dates Visited
L	40°12'	118°33'	8 km N. Lovelock, Nevada.	31 May–2 June 1964; 7–10 July 1964; 3–5 August 1964.
G	38°48'	117°59'	8 km S. Gabbs, Nevada.	5–6 June 1964; 4–7 July 1964; 2–3 August 1964.
V	37°05'	117°15'	40 km NW. Beatty, Nevada.	20–22 May 1964; 1–4 July 1964; 29 July–1 August 1964.
P	36°18'	116°14'	~10 km W. Pahump, Nevada.	15–18 May 1964; 28 June–1 July 1964; 27–29 July 1964.
S	35°18'	114°51'	17 km SSE. Searchlight, Nevada.	13–15 May 1964; 25–27 June 1964; 24–26 July 1964; 12–14 August 1964.
M	35°06'	118°09'	8 km N. Mojave, Calif.	14–17 May 1963; 3–5 June 1963; 22–24 June 1963; 15–18 July 1963; 29–31 July 1963; 12–14 August 1963; 16–17 April 1964; 20–21 April 1964; 20–21 July 1964.
T	34°08'	115°49'	22–23 km E. Twenty-nine Palms, California.	7 April 1963; 26–30 April 1963; 18–22 May 1963; 5–8 June 1963; 25–28 June 1963; 24–28 July 1963; 8–11 August 1963; 30–31 March 1964; 4 April 1964; 15 April 1964; 21–24 July 1964.
W	33°41'	113°26'	29 km SE. Salome, Arizona.	8 April 1963; 15–16 April 1963; 30 April–1 May 1963; 9–13 May 1963; 9–12 June 1963; 20–21 June 1963; 2–3 July 1963; 1–3 August 1963; 28 March 1964; 14 April 1964; 6 May 1964; 12 June 1964.
SM	33°26'	112°01'	Phoenix South Mountain, Maricopa County, Arizona.	210 different days from October 1964 to August 1966.
C	32°57'	111°51'	16 km NW. Casa Grande, Arizona.	12 April 1963; 18 April 1963; 2 May 1963; 4–7 May 1963; 23–29 May 1963; 12–16 June 1963; 19–22 July 1963; 3–7 August 1963; 29 March 1964; 6–10 April 1964; 12 April 1964; 14–17 June 1964; 14–17 August 1964.
PL	29°54'	112°39'	3 km S. Puerto Libertad, Sonora.	11 June 1969.
B	29°38'	112°32'	40 km SE. Puerto Libertad, Sonora.	7–10 June 1969.
H	29°22'	110°59'	65 km N. Hermosillo, Sonora.	29–30 May 1969.
A	28°20'	111°21'	7 km E. Estero de Tastiota, Sonora.	31 May–5 June 1969.

beach-dwelling *Callisaurus d. carmenensis* in Baja California were described in some detail by Tevis (1944). Norris (1948) considered arboreality and stomach contents, and suggested that these lizards climb to avoid extremely high substrate temperatures rather than to obtain food. The dentition of *Callisaurus* was related to its diet by Hotton (1955), who also compared its dentition with that of other iguanids. Information available in the middle of the century was summarized by Smith (1946) and Stebbins (1954). Belkin (1961) reported an average running speed of 7.2 meters per second in seven adults. Clarke (1965) studied behavior and aggressive displays in *Callisaurus*. Cuellar (1966) examined sperm storage structures. The zoogeography and probable past movements of *Callisaurus*

in the Great Basin desert were considered by Banta (1962). Norris and Lowe (1964) and Norris (1967) analyzed background color matching with spectrophotometers. Asplund (1967) presented information on reproduction in a Baja California population. Body temperature relationships of *Callisaurus* have been treated variously by Hunsaker and Johnson (1959), Soulé (1963), Brattstrom (1965), Cunningham (1966), Norris (1967), Porter (1967), Mayhew (1968), Packard and Packard (1970) and Kay (1970). Mays and Nickerson (1968) reported finding individuals asleep on paved roads at night. Fitch (1970) reviewed what is known about reproduction in *Callisaurus*. Kay, Miller and Miller (1970) recently published observations on diet and reproduction in a California population of

TABLE 2. SELECTED RECORDS OF GROWTH AND MOVEMENTS OF RECAPTURED *Callisaurus draconoides* ON AREA SM.

Sex	Capture date	SVL (mm)	Tail (mm)	Growth (mm/day)	Distance between captures (m)
♂	19 Mar 66	41	—	—	—
	16 Jun 66	69	86	0.32	9.1
♀	21 Mar 65	40	52	—	—
	8 Aug 65	68 ¹	82	0.20	35.1
♀	6 Apr 65	43	55	—	—
	23 Jun 65	65	84	0.29	25.1
♀	24 Apr 66	49	62	—	—
	30 May 66	59	74	0.28	19.5
♀	22 May 66	51	46	—	—
	3 Jul 66	56	50	0.12	31.1
♀	6 Apr 66	37	—	—	—
	20 Aug 66	67 ¹	84	0.22	120.0
♀	25 May 66	55	65	—	—
	10 Jul 66	58	70	0.06	11.3

¹ Gravid.

Callisaurus. Telford (1970) reported on its endoparasites.

STUDY AREAS AND METHODS

Observations were made on over a thousand individuals of *Callisaurus* during the springs and/or summers of 1963, 1964, 1965, 1966 and 1969 in Nevada, southern California, Arizona and the Mexican states of Sonora and Baja California. Much of our information is based on 598 specimens which

were actually collected and preserved,* although abundance estimates, microhabitat utilization patterns and movements also incorporate animals that escaped and/or those marked, released and recaptured (below). Fourteen geographically separated flatland desert study areas were selected (Table 1), representing a variety of habitats ranging

* ERP's 475 specimens are deposited in the Los Angeles County Museum of Natural History; WSP's 123 are deposited at Arizona State University (ASU 12258-12380).

TABLE 3. MICROHABITAT LOCATIONS OF UNDISTURBED *Callisaurus* WHEN FIRST SIGHTED (PERCENTAGES).

Area	N	Open		Larrea		Other Shrubs		Trees		Rocks*	
		sun	shade	sun	shade	sun	shade	sun	shade	sun	shade
G,L	23	39.1					4.4				56.4
V	78	83.2		3.8		1.3					11.6
P,S	35	94.3		5.7							
M	33	81.9		12.1	3.0	3.0					
T	37	81.1		8.1	5.4		2.7	2.7			
W	15	86.6		6.7				6.7			
C	54	92.6		5.5		1.9					
PL	17	58.8				17.6	11.8	5.9	5.9		
B	47	70.2		8.5	2.1	17.1		2.1			
H	21	42.9	9.5			14.3				23.8	9.5
A	87	74.7				17.2		6.9	1.2		
Totals	447	77.0	0.4	4.5	0.9	7.2	0.9	2.2	0.4	6.0	0.4

* Small rocks usually around 10 cm. in diameter.

TABLE 4. SUMMARY OF STOMACH CONTENTS OF 104 *Callisaurus* FROM THREE STUDY AREAS (L, G, AND V) IN THE GREAT BASIN DESERT.

Prey Category	Number	Volume	% Total Number	% Total Volume	Frequency
Spiders	11	.9	1.6	1.1	8.7
Solpugids	1	.2	.2	.2	1.0
Ants	96	1.7	14.1	2.0	15.4
Other Hymenoptera	15	1.5	2.2	1.8	7.7
Grasshoppers	116	37.2	17.0	44.1	73.1
Roaches	8	1.8	1.2	2.1	7.7
Mantids	3	1.4	.4	1.7	2.9
Ant Lion Adults	2	.3	.3	.4	1.9
Adult Beetles	242	14.7	35.5	17.4	84.6
Termites	4	.1	.6	.1	1.9
Hemiptera	2	.2	.3	.2	1.9
Diptera	17	1.7	2.5	2.0	14.4
Adult Lepidoptera	4	.6	.6	.7	2.9
Insect eggs	23	.6	3.4	.7	3.8
Pupae	1	.1	.2	.1	1.0
All insect larvae	48	5.1	7.0	6.1	25.0
Unidentified insects	29	2.0	4.3	2.4	21.1
Lizards, sloughed skin	7	.7	1.0	.8	2.9
Floral parts of plants	9	1.4	1.3	1.7	3.8
Vegetative parts, plants	35	5.5	5.1	6.5	15.4
Unidentified materials	9	6.6	1.3	7.8	59.5
TOTALS	682	84.3			

from structurally simple shrub desert with only one perennial plant life form to structurally rather complex Sonoran desert, often with as many as 10 or more different life forms of perennial plants. Descriptions of the climate, fauna, and flora of most of the study areas have been published elsewhere (Pianka, 1966, 1967, 1970; Parker, 1971, 1972).

On area SM, live lizards were trapped, marked, and released using 424 pitfall traps placed irregularly and in a 1.1 hectare grid. Some lizards were marked by toe clipping. On other areas, lizards were observed while observers walked transects through the habitat, recording distances covered with leg pedometers. These walks were usually made during the morning hours, and were almost always begun before *Callisaurus* emerged from their nocturnal retreats. Using the first *Callisaurus* sighted as "time zero," the total number observed was divided by the miles walked to estimate abundance. As the effective width of these transects was estimated at about 6 m, a strip 1.6 km long approximates a hectare. (In the rest of this paper estimated

abundances are converted from the number per man-kilometer to the approximate number per hectare.) Although these estimates are crude, they vary over two orders of magnitude and should at least reflect true densities.

For most lizards encountered, we recorded: date, time, approximate size (small, medium, or large), sex (if possible), and microhabitat position in the environment when first observed. Many lizards were also collected; this material provided additional data on cloacal temperature, sex, wet weight, exact size (snout-vent length, SVL), and whether or not the tail had been broken and regenerated. All SVL and tail lengths were measured on live, or freshly killed, lizards in the field. Dissection of preserved specimens supplied information on gonadal state and stomach contents. Testes lengths of preserved specimens were measured with vernier calipers or metal millimeter rulers, and ratios of mean testis length over SVL were calculated to compensate for differences in body size following Asplund and Lowe (1964). Volumes of oviducal eggs and intact stomachs were esti-

TABLE 5. SUMMARY OF STOMACH CONTENTS OF 185 *Callisaurus* FROM SIX SOUTHERN STUDY AREAS (P, S, M, T, W, AND C) IN THE MOJAVE AND SONORAN DESERTS.

Prey Category	Number	Volume	% Total Number	% Total Volume	Frequency
Spiders	41	2.9	1.9	2.3	14.6
Ants	279	3.9	13.1	3.0	31.4
Other Hymenoptera	55	3.7	2.6	2.9	10.3
Grasshoppers	95	24.0	4.5	18.7	36.7
Roaches	15	5.0	.7	3.9	4.9
Mantids	9	1.2	.4	.9	2.7
Ant Lion Adults	6	.8	.3	.6	3.2
Adult Beetles	627	38.8	29.4	30.2	86.1
Termites	509	9.3	23.8	7.2	10.3
Homoptera—Hemiptera	31	2.2	1.4	1.7	8.1
Diptera	23	3.4	1.3	2.7	12.4
Adult Lepidoptera	1	.1	.1	.1	.5
Insect eggs	6	.1	.3	.1	1.5
All insect larvae	75	6.7	3.5	5.2	18.9
Unidentified insects	154	7.6	7.2	5.9	41.7
Lizards, sloughed skin	4	10.7	.2	8.3	2.7
Floral parts of plants	1	.1	.1	.1	.5
Vegetative parts, plants	192	3.7	9.0	2.9	12.4
Unidentified materials	8	4.2	.4	3.3	27.6
TOTALS	2135	128.4			

mated to one-tenth of a cc by volume displacement using a small narrow-necked graduated cylinder. Estimates were made of the numbers and volumes of items in various prey categories for each lizard stomach. Approximate volumes of individual prey items were estimated visually, to the nearest one-hundredth of a cc, by the proportion of the total stomach volume taken up by a given item. Prey items in each lizard stomach were counted individually, except for termites for which standards were determined and the number per stomach estimated from the volume. Methods employed are discussed in greater detail by Pianka (1965, 1967, 1970) and Parker (1971, 1972).

RESULTS AND DISCUSSION

Movements.—On area SM, 45 individuals were marked and released; 19 of these were recaptured. Mean distance between capture points in seven lizards which were immature at recapture was 20.3 m, while it was 31.9 m in six which were adult. Six other recaptures (excluded from the means) were in the same trap as the original capture. Table 2 gives information on movements and growth of

seven lizards. These are minimum estimates of distances moved as the maximum distance between traps was 122 m.

Microhabitat and Diet.—*Callisaurus* forages in the open spaces between shrubs in typical iguanid fashion, by "sitting-and-waiting" (Pianka, 1966), although they occasionally also actively dig for prey with their fore feet. Table 3 summarizes microhabitat locations of 447 undisturbed lizards when first sighted. The lizards characteristically stand with their head and anterior thorax elevated on straightened forelegs. Such a stance maximizes the lizard's field of view and presumably the efficiency of utilization of open spaces, although it might serve other functions as well. Differences between study areas in lizard microhabitat locations (Table 3) are generally minor; the percentage of lizards in the open (including those on rocks and in the open shade next to plants) varies from 59 to 95%. Although Norris (1948) reported arboreality in *Callisaurus*, we never observed them climbing on anything but rocks and boulders.

In Tables 4, 5, and 6, stomach contents of 469 *Callisaurus* are tabulated. Inspection of these tables shows that the lizards are fairly

TABLE 6. SUMMARY OF STOMACH CONTENTS OF 180 *Callisaurus* FROM FOUR STUDY AREAS IN THE MEXICAN STATE OF SONORA (MAG, PL, A, AND B).

Prey Category	Number	Volume	% Total Number	% Total Volume	Frequency
Spiders	76	1.5	1.5	3.7	30.6
Scorpions	3	0.3	0.1	0.8	1.7
Ants	367	2.8	7.2	7.0	47.8
Other Hymenoptera	147	5.4	2.9	13.3	44.4
Grasshoppers	24	2.6	0.5	6.4	15.6
Roaches	7	0.3	0.1	0.7	3.9
Mantids	7	0.4	0.1	1.0	3.3
Adult Beetles	130	2.4	2.6	6.0	37.8
Termites	121	0.3	2.4	0.7	7.2
Homoptera-Hemiptera	59	0.8	1.1	2.0	23.9
Diptera	23	0.9	0.5	2.1	10.6
Adult Lepidoptera	5	0.4	0.1	0.9	2.2
Insects eggs	15	0.02	0.3	0.1	0.6
All insect larvae	4095	18.8	80.4	46.6	67.2
Unidentified insects	14	1.1	0.3	2.9	23.3
Lizards, sloughed skin	2	0.2	0.04	0.4	1.1
Plant material		0.9		2.2	8.9
Unidentified materials		1.3		3.3	19.4
TOTALS	5095	40.4			

generalized feeders, taking a wide variety of prey. The composition of the diet varies from area to area, during the season, and latitudinally. Grasshoppers dominate the diet during July and August on northern areas (Table 4), and comprise the most important food item on northern areas while beetles and insect larvae are major prey on southern ones (Tables 5 and 6). Some vegetative material is eaten, especially in the spring and on northern areas. The Death Valley population reported on by Kay et al. (1970) certainly seems to be quite atypical in its diet, which consisted largely of Diptera. It is likely that Diptera were particularly common at Saratoga Springs and that *Callisaurus* merely capitalized on their availability. Very few Diptera are eaten by populations of this lizard collected in desert habitats.

Size, Growth, and Age.—We use the following terminology for age groups:

- 1) hatchlings—26–32 mm (less than about 7 days since hatching);
- 2) juveniles—26–50 mm (before first hibernation, including hatchlings);
- 3) immatures—31–62 mm ♀♀ and 31–66 mm ♂♂ (after first hibernation but smaller than minimal size at sexual maturity);
- 4) first year—(all animals in the first year of life including hatchlings, juveniles, and immatures);
- 5) adults—63–87 mm ♀♀ and 67–99 mm ♂♂ (all animals over minimal size at sexual maturity).

Nine first-year animals recaptured at intervals greater than 7 days grew at an average rate of 6.5 mm per month. Detailed observations on area SM allow analysis of annual changes in the composition of a *Callisaurus* population (Fig. 1). July and August hatchlings approach minimum adult size in April or May of the following year. Autumn (September–November) hatchlings apparently grow only a few mm or not at all before hibernating, and thus do not reach minimum adult size until June or July (Fig. 1 and Table 2). Size and age composition of the population on area SM changed markedly during the season (Fig. 1). In spring (February–April), samples contain over 80% immatures and only a few old adults, perhaps partially reflecting greater activity of immatures. By early summer (May–June), many immatures had reached minimum adult size, but over 40% of the sample is composed of immature lizards nearing maturity. In mid-summer (July) over 80% of the sample is adult, with

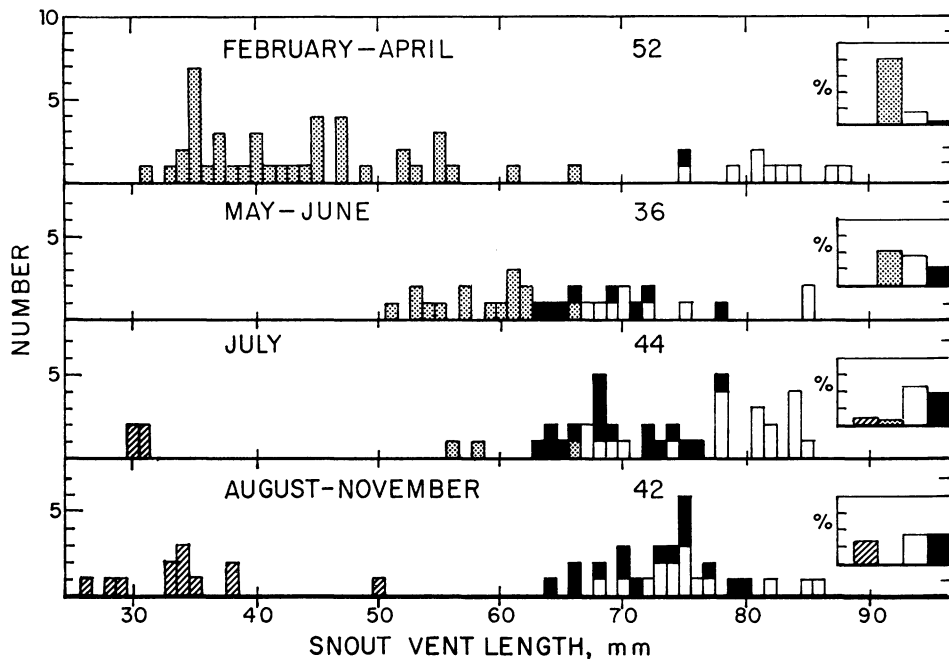


Fig. 1. Frequency distributions of snout-vent lengths and for different age and sex groups on area SM by season. Left ordinate is number of lizards. Each mark on ordinate of percentage histogram is 20%. Numbers indicate sample size. Unshaded = adult male, darkened = adult female, stippled = immature, cross-hatched = juveniles.

only a few immatures remaining. After hatchlings emerge, in late summer and autumn, about 75% of the population are adults and 25% juveniles. These data suggest relatively high annual population turnover on area SM, since adults older than a year constitute less than 20% of the spring sample.

There is a pronounced sexual size dimorphism in *Callisaurus* (Fig. 2), with males attaining considerably larger sizes than females. Although males are larger as adults, they may grow more rapidly than females (Table 2) and hence take no longer to reach sexual maturity. Sex ratios are usually near equality (examine Figs. 1 and 2 and Table 9).

Reproduction.—Yolked ovarian eggs over 3 or 4 mm in diameter occur from April through September. Females had shelled eggs in their oviducts only during June, July, and August; the average volume of an oviducal egg is .36 cc ($N = 41$), and clutch volume averages about 14% of total female body weight ($N = 10$). Apparently, yolk deposition begins in April in old females (i.e., those not hatched the previous year), and they deposit their first clutches in June, judging from the sub-

adult size of all first-year lizards as late as April and from the appearance of hatchlings in mid-July (Fig. 1). Hatchlings grow rapidly (Table 2), with most females reaching 63 mm in snout-vent length (the size of the smallest gravid female observed) at an age of less than a year. Minimum adult size must vary, however, since some females (63–69 mm) collected in July were not in reproductive condition. Most females collected in August were gravid, and two immature females marked in spring were gravid when recaptured in August (Table 2). Thus, a majority of females probably breed in their first year. From two to eight eggs constitute a clutch, but 90% of the lizards have clutches varying only from three to six eggs. The mean of 73 clutches is 4.42 and there is little tendency for larger females to lay larger clutches (Fig. 3). The number of clutches produced annually probably varies with the age of a female. Females sexually mature at the beginning of a breeding season could lay more than one clutch, whereas first-year individuals may lay either one or two clutches, depending upon when they reach maturity. The possibility of multiple clutches is based upon

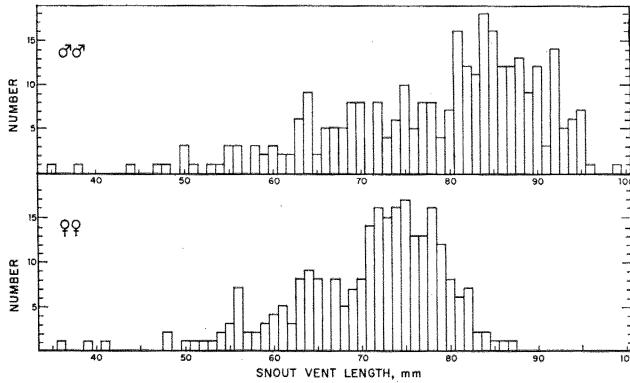


Fig. 2. Frequency distributions of snout-vent lengths of male and female *Callisaurus*, showing the sexual size dimorphism.

Tinkle's (1961) criteria, but we were unable to find any other indication that individual females lay more than a single clutch per season. None of the 73 gravid females examined contained both shelled oviducal eggs

and yolked ovarian follicles simultaneously. It is thus possible that the five month occurrence of gravid females merely represents the progressive maturation of immature females with passage of the breeding season, rather than continued oviposition by females which had already laid one clutch.

Since various aspects of the timing and success of reproduction, including clutch size, of desert lizards have frequently been related to recent precipitation (Hoddenbach and Turner, 1968; Mayhew, 1967; Pianka, 1965, 1970; Zweifel and Lowe, 1966), we compared clutch size on different study areas with various statistics of precipitation (Table 7). However, we found no correlations with either long-term or short-term precipitation values, perhaps because of small sample sizes.

In the Sonoran desert, male *Callisaurus* emerge in March with small testes (Fig. 4). Enlargement begins in April, and a nearly constant relative size is maintained through June. Maximum size is reached in July and early August, with an apparent drop in late August. Enlargement of vasa deferentia and epididymides lags somewhat behind testes. In the Mojave and Great Basin deserts, testes decrease in size sharply in late July, suggesting a shorter breeding season.

Males reach sexual maturity at slightly larger sizes than females. Kay et al. (1970) suggested that males reach sexual maturity at 70 mm SVL. Several of our males between 60-66 mm had moderately enlarged testes from April through July, but vasa deferentia and epididymides were minute. The smallest male with both enlarged testes and vasa

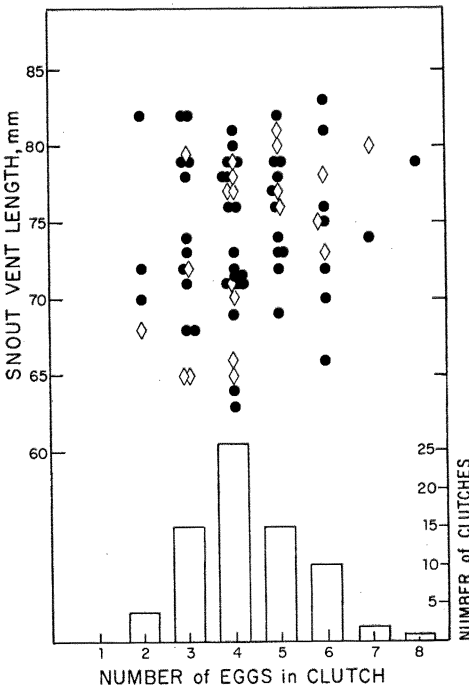


Fig. 3. Clutch size is plotted against female snout-vent length. Histogram at bottom shows the frequency distribution of sizes of 73 clutches. Oviducal eggs plotted as open diamonds, enlarged yolked ovarian follicles as closed circles. Mean clutch size from these data is 4.42 eggs.

TABLE 7. NUMBER OF ADULT FEMALES EXAMINED, NUMBER OF CLUTCHES, PERCENTAGE OF FEMALES WITH ENLARGED EGGS, MEAN CLUTCH SIZE, ESTIMATED NUMBER OF LIZARDS PER HECTARE, PERCENTAGE COVERAGE STATISTICS FROM PLANT QUADRAT MEASUREMENTS,* AND TWO SETS OF PRECIPITATION STATISTICS, ONE FOR THE TOTAL YEAR AND ONE FOR THE GROWING SEASON, INCLUDING LONG TERM MEAN ANNUAL PRECIPITATION (LTM), IN CM, SHORT TERM MEAN PRECIPITATION DURING THE FIVE YEARS (STM₅) AND THE YEAR (STM₁) IMMEDIATELY PRIOR TO STUDY.

Area	Number of ♀♀	No. of Clutches	Percent Gravid	Mean Clutch	Abundance	% Coverage		Total Year			Growing Season		
						\bar{X}	S	LTM	STM ₅	STM ₁	LTM	STM ₅	STM ₁
L	7	1	14	5.0	.192	6.0	1.2	14.0	14.8	23.7	3.3	4.5	7.4
G	1	1	100	6.0	.020	14.8	2.0	9.6	9.2	10.7	2.9	7.2	6.5
V	36	6	17	3.8	1.750	10.8	2.2	11.6	9.9	12.7	2.8	3.2	7.9
P	15	6	40	3.3	.494	9.1	2.1	9.3	8.7	9.3	3.5	2.6	4.6
S	0	—	—	—	.091	10.3	3.4	18.7	14.1	13.5	10.5	8.1	9.6
M-63	14	2	14	2.5	.455	13.3	3.3	12.7	10.9	16.0	1.3	1.0	0.2
M-64	1	1	100	3.0	.316	13.3	3.3	12.7	10.2	9.7	1.3	2.4	7.7
T-63	20	9	45	3.8	.660	9.1	3.6	9.4	8.6	4.7	7.1	5.9	3.4
T-64	3	1	33	6.0	.110	9.1	3.6	9.4	9.8	16.6	7.1	8.0	15.3
W	7	1	14	3.0	.370	9.3	5.7	19.2	12.9	14.1	11.4	6.5	12.6
SM	35	19	54	4.5	—	—	—	18.6	14.8	16.7	10.8	8.7	14.9
C-63	16	5	31	5.8	.880	10.5	9.0	20.9	18.5	15.1	13.1	11.4	7.8
C-64	13	8	62	4.6	.701	10.5	9.0	20.9	19.4	26.2	13.1	13.2	17.4
B	21	11	52	4.5	high	—	—	10.6	12.6	—	10.6	12.6	—
A	43	2	5	4.5	high	—	—	19.0	17.9	17.0	19.0	17.9	17.0
Total	232	73	31	4.4									

* Taken from Pianka (1970).

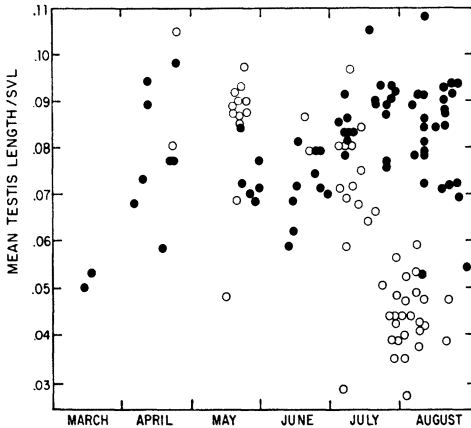


Fig. 4. Seasonal changes in the ratio of mean testis size over SVL of adult male *Callisaurus draconoides* (67 mm SVL and over) in the Sonoran desert (areas C and SM—closed dots) and in the Mojave and Great Basin deserts (areas Y, V, and L—open dots). Each dot represents the mean of both testes for a given male. Note apparent May peak and sharp testicular drop in late July in northern lizards, suggesting a shorter breeding season.

deferentia was 67 mm. Size at sexual maturity is probably variable in males as well as in females. As with females, percentages of mature males in one population (area SM) gradually increased to a maximum in late summer (Fig. 1).

Mating seemingly begins in May for older males and reaches a peak in August. We never observed copulation, but the majority of adults of both sexes have bright breeding colors from June through August.

Hatchlings appeared from 14 July through 30 November on area SM. Judging from the large number of hatchling-sized young collected in February and March (Fig. 1) and the high frequency of gravid females in August, the greatest numbers of young must have hatched in October and November of the previous year even though only a few were seen or collected then.

Fitch (1970) suggested a north-south trend of increasing length of breeding season and number of clutches laid by an individual *C. draconoides* in one year. Our data and that of Kay et al. (1970) on the same species in Death Valley, California, support this contention. Enlarged testes and possibly egg laying extended over four months at Phoenix versus two months in Death Valley, even though the species' seasonal activity is similar

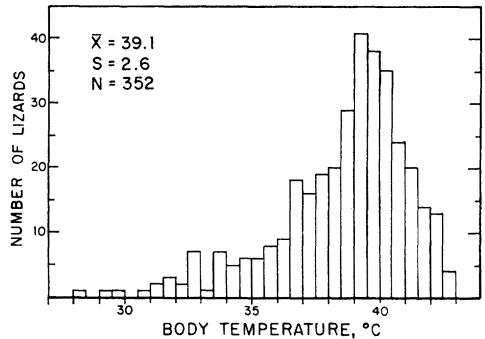


Fig. 5. Frequency distribution of body temperatures of 352 active *Callisaurus*.

at both locations. Differences may, however, also be partially due to differences in collecting methods and presentation of data, or perhaps due to the occurrence of an atypical year at one of the locations.

Abundance.—*Callisaurus* is usually a fairly uncommon desert lizard; our study areas are no exception, and on many of them it was rare. As the estimates of abundance vary by two orders of magnitude (Table 7), we looked for correlations with abundance. Because these lizards are so often first sighted in the open spaces between plants (Table 3), a first hypothesis was that percentage coverage of perennial vegetation might control their abundance. However, examination of Table 7 shows that this is not true. Statistically significant correlations between abundance and various precipitation parameters occur in *Uta stansburiana* (Pianka, 1965) and in *Cnemidophorus tigris* (Pianka, 1970). There is, however, no significant correlation between any of the precipitation figures listed in Table 7 and *Callisaurus* abundance. Although the above results are negative, they serve to demonstrate that neither of these apparently important environmental attributes seems to regulate *Callisaurus* abundance.

Thermoregulation.—Figure 5 shows the frequency distribution of body temperatures (BTs) of 352 active *Callisaurus* ($\bar{X} = 39.1$, $S = 2.6$), which is in close agreement with values reported in the literature (Brattstrom, 1965; Cunningham, 1966; Mayhew, 1968; Soulé, 1963; Packard and Packard, 1970). Although the sample size is too small for significance, BTs of lizards in the shade when first sighted ($\bar{X} = 40.0$, $S = 1.6$, $N = 15$) aver-

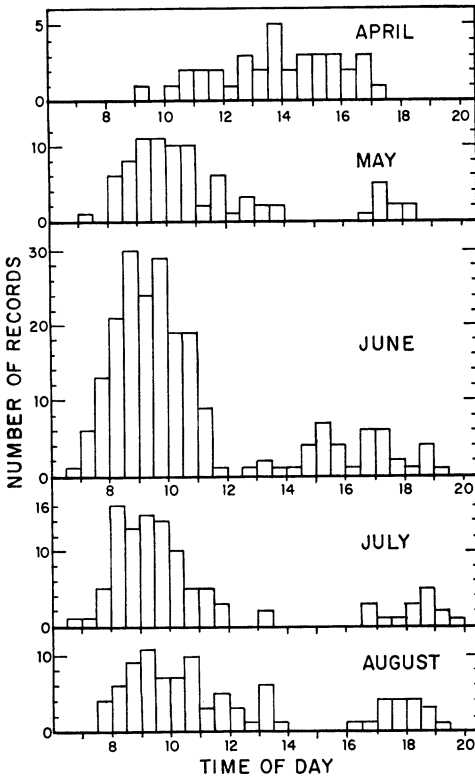


Fig. 6. Frequency distributions of times of collection, by months, showing the seasonal change in onset of time of activity.

age a full degree Centigrade higher than those of animals in the sun ($\bar{X} = 39.0, S = 2.6, N = 334$). There is a loose positive correlation between air temperature and body temperature, which almost always exceeds air temperature, often by as much as 10 C and occasionally by 15 C. Packard and Packard (1970) found a very tight positive correlation between substrate temperatures and BTs in *Callisaurus*.

Using the technique of Licht et al. (1966), preferred body temperatures (PBTs) were measured in a thermal gradient on four newly-captured individuals over several entire daily periods of activity at 15 minute intervals; the following statistics were obtained ($\bar{X} = 38.1, S = 1.8, N = 807$). BT and PBT statistics are significantly different ($P < .01$) using the t-test (means) and an F-test (variances), suggesting that, in nature, the lizards may accept both more variable and higher BTs.

During the cool spring months, *Callisaurus*

TABLE 8. FREQUENCIES OF BROKEN REGENERATED TAILS BY SIZE CLASS AND SEX, FOR THE ELEVEN SOUTHERN STUDY AREAS (MOJAVE AND SONORAN DESERTS).

Size Class	N	Number Broken	Percentage Broken
26-40 mm	35	5	14.3
41-50 mm	21	4	19.1
51-60 mm	54	13	24.1
Females			
61-70 mm	66	12	18.2
71-80 mm	104	29	27.9
81-90 mm	19	12	63.0
Males			
61-70 mm	45	5	11.1
71-80 mm	45	9	20.0
81-90 mm	103	24	23.3
91-99 mm	33	14	42.4

do not emerge until late morning (~0900 to 1030), whereas in the warm summer months they are active as early as 0730 hours. Figure 6 illustrates this seasonal change in the onset

TABLE 9. PERCENTAGES OF BROKEN AND REGENERATED TAILS, AND SAMPLE SIZES, ON VARIOUS STUDY AREAS, FOR EACH SEX AND FOR THE SEXES COMBINED.

Area	Latitude	Number of		% Broken tails		Total
		males	females	males	females	
G, L	39°40'	14	8	7	13	9.1
V	37°05'	45	36	20	3	12.4
P	36°18'	20	15	20	27	22.9
S	35°18'	2	0	50	—	50.0
M-63	35°06'	13	14	8	21	14.8
M-64	35°06'	5	1	0	0	0.0
T-63	34°08'	12	20	25	40	34.4
T-64	34°08'	3	3	0	33	16.7
W	33°41'	9	7	11	43	25.0
SM	33°26'	56	45	29	29	28.7
C-63	32°57'	13	16	8	25	17.2
C-64	32°57'	15	13	40	23	32.1
PL	29°54'	8	9	13	11	11.8
B	29°38'	27	21	33	29	31.3
H	29°22'	12	10	25	40	31.8
A	28°20'	51	43	18	21	19.2
North (G,L,V)		59	44	17	5	11.7
South (All others)		246	217	22	27	24.6
Total		305	261	21	23	22.3

TABLE 10. SUMMARY OF MAJOR ASPECTS OF REPRODUCTION IN *Callisaurus draconoides* AND RELATED LIZARDS.

Species	Location	Mean Clutch Size	Period of Egg Laying	Maximum Testis Size	Age At Maturity (Years)	Minimum SVL At Maturity (mm)	Authority
						♂	♀
<i>Callisaurus draconoides</i>	California	(2-5)	Jun-Jul	May-Jun	—	70	65
<i>Callisaurus draconoides</i>	Northern (Areas L, G, V)	4.2	—	May-Jun	—	—	—
<i>Callisaurus draconoides</i>	Southern (Areas P, S, M, T, W, C, & SM)	4.3	May-Aug	July-Aug	1	67	63
<i>Callisaurus draconoides</i>	Sonora, Mexico (Areas A & B)	4.5	—	—	—	—	—
<i>Holbrookia lacerata</i>	Texas	(4-12)	May-Aug	—	—	—	—
<i>Holbrookia maculata</i>	Texas	6.1	—	—	1	—	45
<i>Holbrookia maculata</i>	Kansas	4.9	May-Aug	—	—	—	—
<i>Holbrookia maculata</i>	Arizona & Mexico	7.0	Apr-Sep	—	—	—	—
<i>Holbrookia texana</i>	Texas	5.3	Jun-Aug	—	—	53	55
<i>Holbrookia texana</i>	Texas	5.0	Apr-Aug	—	—	—	48
<i>Uma inornata</i>	California	2.4	May-Sep	Apr-May	1-2	80	70
<i>Uma notata</i>	California	2.0	May-Aug	Apr-May	1-2	80	70
<i>Uma scoparia</i>	California	2.6	May-Jul	Apr-May	1-2	80	70

of activity, and, in addition, the figure suggests a bimodal diel period of activity although of course this is uncertain without correction for diurnal variation in sampling effort. Similar seasonal shifts in time of activity have now been reported for many other lizard species (Mayhew, 1964, 1968; Pianka, 1969, 1971a; Tinkle, 1967).

Predation and Broken Tails.—Tables 8 and 9 present, by sex, percentages of naturally broken and regenerated tails which occurred in various size groups and samples. The frequency of broken regenerated tails increases with size (Table 8), perhaps because older lizards have had more contacts with predators. There is a loose positive correlation between the frequency of broken tails in males and *Callisaurus* abundance (Table 7), but no such relationship exists with percentages of broken tails in female lizards. The incidence of broken tails in females is significantly higher in the south than in the north (Chi-square test, $P < .05$), suggesting that predator pressures are higher. Pianka (1965, 1967, 1970) reports similar latitudinal shifts in broken tail frequencies in *Uta stansburiana*, *Phrynosoma platyrhinos*, and *Cnemidophorus tigris*, and gives supporting data on predator abundances which may apply to the present case as well.

Some Comparisons with Other Lizard Species.—Reproductive cycles of *Callisaurus*, *Holbrookia*, and *Uma* are generally similar in that a reproductive peak occurs in late spring and/or summer—a type of cycle characteristic of many North Temperate lizards. Within this apparently natural taxonomic group, however, a number of differences in reproductive parameters do exist. Major differences between the *Callisaurus-Holbrookia* complex and *Uma* are as follows (see Table 10):

- 1) Average clutch size in *Callisaurus* and *Holbrookia* is 2–3 times the clutch size of *Uma*.
- 2) Age at first breeding is one year or less in *Callisaurus* and *Holbrookia* in contrast to probable maturity at two years for most *Uma* (Mayhew, 1968).
- 3) *Callisaurus* and *Holbrookia* reach sexual maturity at consistently smaller body sizes than *Uma*.

The salient similarity between the *Callisaurus-Holbrookia* group and *Uma* is the oc-

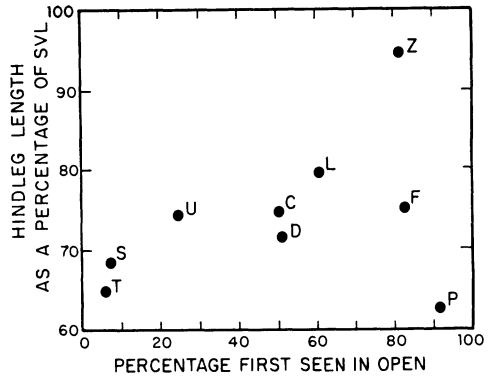


Fig. 7. Plot of mean hindleg length, as a percentage of SVL (from Table 2), against the percentage of lizards first sighted in the open spaces between plants. C = *Cnemidophorus tigris*, D = *Dipsosaurus dorsalis*, F = *Uma scoparia*, L = *Crotaphytus wislizeni*, P = *Phrynosoma platyrhinos*, S = *Sceloporus magister*, T = *Urosaurus graciosus*, U = *Uta stansburiana*, and Z = *Callisaurus draconoides*. Excluding the aberrant *Phrynosoma*, the correlation is significant at the 5% level ($r = .746$, d.f. = 7).

currence of multiple clutches which leads to similarities in duration of egg laying (2–5 months). The occurrence of multiple clutches, usually associated with early-maturing species (Tinkle et al., 1970), sets off the *Callisaurus-Holbrookia-Uma* group from some other North American desert iguanids such as *Dipsosaurus dorsalis* (Mayhew, 1971) and *Phrynosoma solare* (Blount, 1929; Parker, 1971) which are probably single-brooded, late-maturing species. More detailed comparison requires further knowledge of general reproductive phenomena in species of *Holbrookia* and a clarification of the age at maturity of *Uma*. It is likely from the limited available data, however, that reproductive phenomena reflect the population characteristics of the three genera. Judging from their long breeding season, moderate clutch size, and early maturity, *Callisaurus* and *Holbrookia* probably have a rapid population turnover and low longevity. *Uma*, on the other hand, judging from their small clutch size and probable delayed maturity, may have a relatively low population turnover with concomitant increased longevity. Some *Callisaurus* and *Holbrookia* populations might, however, have reduced turnover in the northern parts of their geographic ranges, as is known in *Uta stansburiana* (Tinkle, 1967, 1969; Tanner,

TABLE 11. STATISTICS ON FORELEG AND HINDLEG LENGTHS (EXPRESSED AS PERCENTAGE OF SVL) FOR NINE SPECIES OF NORTH AMERICAN IGUANID LIZARDS.

Species	Foreleg				Hindleg			
	\bar{X}	S	SE	N	\bar{X}	S	SE	N
<i>Dipsosaurus dorsalis</i>	37.4	2.1	.25	70	71.8	4.7	.56	70
<i>Sceloporus megister</i>	46.9	4.7	.51	85	68.4	7.0	.76	85
<i>Crotaphytus wislizeni</i>	40.5	1.9	.15	154	79.6	3.6	.29	154
<i>Urosaurus ornatus</i>	40.3	2.0	.19	112	64.1	3.1	.29	116
<i>Urosaurus graciosus</i>	40.8	5.8	.99	34	64.8	4.5	.76	35
<i>Uta stansburiana</i>	43.6	3.0	.17	312	74.1	4.9	.30	311
<i>Phrynosoma platyrhinos</i>	48.1	2.2	.17	164	62.5	3.0	.23	164
<i>Uma scoparia</i>	45.8	2.1	.31	44	74.8	4.0	.61	44
<i>Callisaurus draconoides</i>	54.5	3.0	.18	274	94.3	5.4	.32	276

1965) and *Cnemidophorus tigris* (Pianka, 1970).

When expressed as a percentage of SVL, both foreleg and hindleg lengths of *Callisaurus* are significantly (t-tests, $P < .001$) longer than the same measures on eight other species of iguanids (Table 11). Figure 7 shows the relationship between hindleg length and the percentage of lizards first sighted in the open spaces between plants for nine sympatric North American lizard species [latter values from Pianka (1970)]. Excluding *Phrynosoma*, whose cryptic behavior and unique body form doubtless make it exceptional, the correlation of mean hindleg length with the percentage of the animals first sighted in the open is significant at the 5% level ($r = .764$). A similar correlation has been found in the Australian skink genus *Ctenotus* (Pianka, 1969).

TABLE 12. STATISTICS ON HINDLEG LENGTHS (EXPRESSED AS A PERCENTAGE OF SVL) FOR TWELVE SPECIES OF AUSTRALIAN *Amphibolurus*.

Species	\bar{X}	S	SE	N
<i>Amphibolurus barbatus</i>	59.0	6.5	.72	81
<i>Amphibolurus inermis</i>	59.1	4.2	.33	158
<i>Amphibolurus reticulatus</i>	63.4	5.4	.82	44
<i>Amphibolurus clayi</i>	68.6	2.9	1.19	6
<i>Amphibolurus muricatus</i>	74.7	3.1	1.25	6
<i>Amphibolurus pictus</i>	79.8	6.8	1.64	17
<i>Amphibolurus scutulatus</i>	89.2	4.1	.43	88
<i>Amphibolurus dualis</i>	90.5	5.1	.91	32
<i>Amphibolurus caudicinctus</i>	91.3	4.5	.71	40
<i>Amphibolurus cristatus</i>	98.6	4.0	1.78	5
<i>Amphibolurus isolepis</i>	99.8	6.2	.27	520
<i>Amphibolurus fordii</i>	104.9	4.8	.46	105

Many phylogenetically disparate, but apparently ecologically similar, desert lizards have converged to varying degrees on a body form close to that of *Callisaurus*. The lacertid *Aporosaura anchietae* from the Namib desert in South West Africa is strikingly reminiscent of *Callisaurus*, even to the banded tail [figured by Mertens (1955; page 145)]. *Aporosaura* is, however, a considerably smaller lizard than *Callisaurus*, with an adult SVL of only about 57 mm. A 55 mm specimen had a hindleg of 42 mm, or 76% of SVL, which proportionately is among the longest of hindlegs in South African lacertids (Fitzsimons, 1943).

A number of Australian desert agamids are also variously convergent. Pianka (1971a) described the ecology of *Amphibolurus isolepis* and noted that this long-legged species makes heavy use of the open spaces between plants; its diet, however, differs markedly from that of *Callisaurus*, consisting of 51.4% ants by volume. Several other *Amphibolurus* closely related to *A. isolepis*, such as *A. fordii* and *A. dualis*, are also somewhat similar to *Callisaurus*, particularly in their place niches. *A. fordii* has a very long hindleg and eats about 50% ants by volume. Two other agamids which can be compared with *Callisaurus* are *Amphibolurus scutulatus* and *A. cristatus* (Pianka, 1971b), both of which forage in the open and have relatively long hindlegs compared to other species of *Amphibolurus* (Table 12). However, the food niche of *A. scutulatus* differs somewhat from that of *Callisaurus*, with its major prey being ants and termites (Pianka, 1971b). Although its ecology is incompletely known, *A. cristatus* is probably the best "ecological equivalent" of

Callisaurus in Australia. *A. cristatus* is a large, sexually dimorphic, species, with a banded tail and a hindleg 98.6% SVL; a small sample of five stomachs contained 48% grasshoppers and 6% beetles by volume (Pianka, 1971b).

ACKNOWLEDGMENTS

The senior author is greatly indebted to his hard-working field assistants: Nicholas Pianka, William Shaneyfelt, and Michael Thomas. Virginia J. Denniston assisted him in numerous ways over the last three years. Computer centers at the University of Washington (Seattle) and the University of Texas at Austin provided the use of their facilities and computer time. His research has been supported by grants from the National Institutes of Health and the National Science Foundation (grant numbers GB-5216, GB-8727 and GB-31006).

The junior author is grateful to Stanley C. Williams for encouragement and field assistance and to W. L. Minckley for guidance and advice. William S. Brown, Harold F. Hirth, and Fenton R. Kay made helpful comments on an earlier manuscript. His wife, Terry, assisted in the field and with typing. He also thanks Ronald Altig, Henry S. Fitch, M. J. Fouquette, Jr., and Walter K. Taylor for assistance and advice. Most of his contribution to this paper (area SM) stems from a Master's thesis submitted at Arizona State University.

LITERATURE CITED

- ASPLUND, K. K. 1967. Ecology of lizards in the relictual cape flora, Baja California. *Amer. Midl. Natur.* 77:462-475.
- , AND C. H. LOWE. 1964. Reproductive cycles of the iguanid lizards *Urosaurus ornatus* and *Uta stansburiana* in southeastern Arizona. *J. Morphol.* 115:27-33.
- ATSATT, S. R. 1939. Color changes as controlled by temperature and light in the lizards of the desert regions of southern California. *Pub. Univ. Calif. L. A., Biol. Sci.* 1:237-276.
- AXTELL, R. W. 1956. A solution to the long-neglected *Holbrookia lacerata* problem and the description of two new subspecies of *Holbrookia*. *Bull. Chicago Acad. Sci.* 10:163-179.
- BANTA, B. H. 1962. Preliminary remarks upon the zoogeography of the lizards inhabiting the Great Basin of the Western United States. *Wasmann J. Biol.* 20:253-287.
- BELKIN, D. A. 1961. The running speeds of the lizards *Dipsosaurus dorsalis* and *Callisaurus draconoides*. *Copeia* 1961:223-224.
- BLOUNT, R. F. 1929. Seasonal cycles of the interstitial cells in the testis of the horned toad (*Phrynosoma solare*). *J. Morphol.* 48:317-344.
- BRATTSTROM, B. H. 1965. Body temperatures of reptiles. *Amer. Midl. Natur.* 73:376-422.
- CAGLE, F. R. 1950. Notes on *Holbrookia texana* in Texas. *Copeia* 1950:230.
- CLARKE, R. F. 1965. An ethological study of the iguanid lizard genera *Callisaurus*, *Cophosaurus*, and *Holbrookia*. *Emporia State Res. Stud.* 13:1-66.
- CUELLAR, O. 1966. Oviducal anatomy and sperm storage structures in lizards. *J. Morphol.* 119:7-20.
- CUNNINGHAM, J. D. 1966. Additional observations on the body temperatures of reptiles. *Herpetologica* 22:184-189.
- FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. *Misc. Pub. Univ. Kans. Mus. Natur. Hist.* 52:1-247.
- FITZSIMONS, V. F. 1943. The lizards of South Africa. *Transvaal Mus. Mem., Pretoria, South Africa, No. 1.*
- GATES, G. O. 1957. A study of the herpetofauna in the vicinity of Wickenburg, Maricopa County, Arizona. *Trans. Kans. Acad. Sci.* 60:403-418.
- HODDENBACH, G. A., AND F. B. TURNER. 1968. Clutch size of the lizard *Uta stansburiana* in southern Nevada. *Amer. Midl. Natur.* 80:262-265.
- HOTTON, N. 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. *Ibid.* 53:88-114.
- HUNSAKER, D., AND C. JOHNSON. 1959. Internal pigmentation and ultraviolet transmission of the integument in amphibians and reptiles. *Copeia* 1959:311-315.
- JOHNSON, C. 1960. Reproductive cycle in females of the greater earless lizard, *Holbrookia texana*. *Copeia* 1960:297-300.
- JOHNSON, D. H., M. D. BRYANT AND A. H. MILLER. 1948. Vertebrate animals of the Providence Mountains area of California. *Univ. Calif. Pub. Zool.* 48:221-376.
- KAY, F. R. 1970. Environmental responses of active lizards at Saratoga Springs, Death Valley, California. *Great Basin Natur.* 30:146-165.
- , B. W. MILLER AND C. L. MILLER. 1970. Food habits and reproduction of *Callisaurus draconoides* in Death Valley, California. *Herpetologica* 26:431-436.
- KLAUBER, L. M. 1939. Studies of reptile life in the arid southwest. *Bull. Zool. Soc. San Diego* 14:1-100.
- KNOWLTON, G. F. 1938. Lizards in insect control. *Ohio J. Sci.* 38:235-238.
- , AND W. L. THOMAS. 1934. Notes on some insectivorous Utah lizards. *Proc. Utah Acad. Sci., Arts, Lett.* 11:257-259.
- , AND C. F. SMITH. 1935. The desert grid-iron-tailed lizard. *Copeia* 1935:103.
- LICHT, P., W. R. DAWSON, V. H. SHOEMAKER AND A. R. MAIN. 1966. Observations on the thermal relations of Western Australian lizards. *Copeia* 1966:97-110.
- MAYHEW, W. W. 1964. Taxonomic status of California populations of the lizard genus *Uma*. *Herpetologica* 20:170-183.

- . 1965. Reproduction in the sand-dwelling lizard *Uma inornata*. *Herpetologica* 21:39-55.
- . 1966a. Reproduction in the psammophilous lizard *Uma scoparia*. *Copeia* 1966:114-122.
- . 1966b. Reproduction in the arenicolous lizard *Uma notata*. *Ecology* 47:9-18.
- . 1967. Comparative reproduction in three species of the genus *Uma*, p. 45-61. In: *Lizard Ecology: A Symposium*. W. W. Milstead, ed. Univ. Missouri Press, Columbia, Mo.
- . 1968. Biology of desert amphibians and reptiles, p. 195-356. In: *Desert Biology*. G. W. Brown, ed. Academic Press, New York.
- . 1971. Reproduction in the desert lizard, *Dipsosaurus dorsalis*. *Herpetologica* 27:57-77.
- MAYS, C. E., AND M. A. NICKERSON. 1968. Nocturnal behavior in iguanid lizards and possible correlation with roadkills. *Herpetologica* 24:258-259.
- MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Univ. California Press, Berkeley.
- MOSAUER, W. 1932. Adaptive convergence in the sand reptiles of the Sahara and of California. *Copeia* 1932:72-78.
- . 1936. The toleration of solar heat in desert reptiles. *Ecology* 17:56-66.
- NORRIS, K. S. 1948. Arboreal feeding habits and feeding of the grid-iron tailed lizard. *Herpetologica* 4:217-218.
- . 1967. Color adaptation in desert reptiles and its thermal relationships, p. 162-229. In: *Lizard Ecology: A Symposium*. W. W. Milstead, ed. Univ. Missouri Press, Columbia, Mo.
- , AND C. H. LOWE, JR. 1964. An analysis of background color matching in amphibians and reptiles. *Ecology* 45:565-580.
- PACK, H. J. 1923. Food habits of *Callisaurus ventralis ventralis* (Hallowell). *Proc. Biol. Soc. Wash.* 36:79-82.
- PACKARD, G. C., AND M. J. PACKARD. 1970. Ecritic temperatures of zebra-tailed lizards on the Mojave desert. *Herpetologica* 26:168-172.
- PARKER, W. S. 1971. Ecological observations on the regal horned lizard (*Phrynosoma solare*) in Arizona. *Herpetologica* 27:333-338.
- . 1972. Aspects of the ecology of a Sonoran Desert population of the western banded gecko, *Coleonyx variegatus* (Sauria, Eublepharinae). *Amer. Midl. Natur.*, *in press*.
- PIANKA, E. R. 1965. Species diversity and ecology of flatland desert lizards in western North America. Ph.D. Thesis, University of Washington, Seattle, Washington (Univ. Microfilms No. 66-5867).
- . 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47:1055-1059.
- . 1967. On lizard species diversity: North American flatland deserts. *Ecology* 48:333-351.
- . 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* 50:1012-1030.
- . 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:705-720.
- . 1971a. Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. *Copeia* 1971:527-536.
- . 1971b. Notes on the biology of *Amphibolurus scutulatus* and *Amphibolurus cristatus*. *West. Australian Natur.* 12:36-41.
- PORTER, W. P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecol. Monogr.* 37:273-296.
- SMITH, H. M. 1946. *Handbook of Lizards*. Cornell Univ. Press (Comstock), Ithaca, New York.
- SOULÉ, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. *Copeia* 1963:107-115.
- STEBBINS, R. C. 1954. *Amphibians and reptiles of western North America*. McGraw-Hill Book Co., Inc., New York.
- TANNER, W. W. 1965. A comparative population study of small vertebrates in the uranium areas of the Upper Colorado River Basin of Utah. *Brigham Young Univ. Sci. Bull.* 7:1-31.
- TELFORD, S. R., JR. 1970. A comparative study of endoparasitism among some southern California lizard populations. *Amer. Midl. Natur.* 83:516-554.
- TEVIS, L., JR. 1944. Herpetological notes from Lower California. *Copeia* 1944:6-18.
- TINKLE, D. W. 1961. Population structure and reproduction in the lizard *Uta stansburiana stejnegeri*. *Amer. Midl. Natur.* 66:206-234.
- . 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Pub. Mus. Zool., Univ. Mich.* No. 132.
- . 1969. Evolutionary implications of comparative population studies in the lizard *Uta stansburiana*. In: *Systematic Biology*, Pub. 1692. *Nat. Acad. Sci., Washington, D. C.*
- , H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24:55-74.
- VAN DENBURGH, J. 1922. The reptiles of western North America. *Occ. Pap., Calif. Acad. Sci.* No. 10.
- ZWEIFEL, R. G., AND C. H. LOWE, JR. 1966. The ecology of a population of *Xantusia vigilis*, the desert night lizard. *Amer. Mus. Novitates* 2247:1-57.

DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF TEXAS AT AUSTIN, AUSTIN, TEXAS 78712, AND DEPARTMENT OF BIOLOGY, THE UNIVERSITY OF UTAH, SALT LAKE CITY, UTAH 84112.