

## ECOLOGICAL OBSERVATIONS ON THE LEOPARD LIZARD (*CROTAPHYTUS WISLIZENI*) IN DIFFERENT PARTS OF ITS RANGE

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**ABSTRACT:** Various aspects of the ecology of the leopard lizard, *Crotaphytus wislizeni*, were studied through much of its geographic range, primarily from collection and preservation of specimens. A northern population in Utah was studied in more detail, using mark-release techniques. Leopard lizards exhibited a relatively low diversity of time of activity compared to sympatric lizard species. Cloacal temperatures of 183 active *C. wislizeni* in nature averaged 37.4° C and were significantly warmer than temperatures selected in a laboratory thermal gradient. Patterns of clutch size were irregular, but there was a trend toward larger clutches in the south. Clutch size was correlated with ♀ snout-vent length, and averaged 5.3 ( $N = 94$ ). Reproductive effort (wet weight of eggs/wet weight of gravid ♀) remained relatively constant with age, and was higher in the north. Expenditure per progeny (wet weight of one egg/wet weight of gravid ♀) decreased with snout-vent length and age and was higher in the north. Limited data suggest that reproductive effort, expenditure per progeny, and clutch size may decrease in the oldest ♀♀. Only one clutch is laid annually in northern populations; perhaps two or more are deposited in the south. Testicular regression begins earlier in the south than in the north, but breeding season length is similar in both areas. In Utah, both sexes reach sexual maturity at about 22 months. Minimum adult survivorship in Utah is approximately 50% per year, while minimal annual juvenile survivorship is about 5-6%. Southern adults are significantly larger than northern ones, and this appears to be related to food habits. Southern leopard lizards consume mostly other lizards, while those in the north eat primarily grasshoppers. Ecological characteristics of several species of lizards in the genus *Crotaphytus* are briefly summarized and discussed.

THE leopard lizard, *Crotaphytus wislizeni*, occurs throughout most of the Great Basin, Mojave, Sonoran, and Chihuahuan deserts, in southeastern Oregon, southern Idaho, most of Nevada, Utah, Arizona and New Mexico, southeastern California, western Texas, as well as Baja California, northwestern Sonora, eastern Chihuahua, and western Coahuila in Mexico. Here we examine the ecology of *C. wislizeni* in as much detail as possible, combining information from the literature with new data from our own studies in the states of Idaho, Utah, Nevada, California, Arizona, New Mexico, Sonora, and Baja California. Various aspects of the biology of the species in different geographic areas have been reported by Richardson (1915), Camp (1916), Bentley (1919), Ortenburger and Ortenburger (1926), Stuart (1932), Linsdale (1938), Klauber (1939), Atsatt (1939), Cowles (1941), Fautin (1946), Smith (1946), Johnson et al. (1948), Stebbins (1954), Gates (1957), Tinkle (1959), Woodbury (1959), Banta (1962a, 1967), Jorgensen and Orton (1962), Miller and

Stebbins (1964), Pianka (1965, 1966, 1967, 1973), and Pianka and Pianka (1970). Food habits in Utah were reported by Pack (1922), Knowlton (1934, 1938, 1948, 1974), Knowlton and Janes (1932, 1934), and Knowlton and Thomas (1934a, b, 1936), and in Texas by Milstead and Tinkle (1969). Hotton (1955) described the relationship of dentition to diet based on the series of papers by Knowlton. Jorgensen and Tanner (1963) and Wever et al. (1966) discussed vocalization and hearing. Temperature relations have been mentioned by Cowles and Bogert (1944), Brattstrom (1965), and Cunningham (1966). Aspects of reproduction were included by Ruthven and Stuart (1932), Shaw (1952), Robison and Tanner (1962), and Fitch (1970). Zoogeography was discussed by Banta (1962b), and a fossil described by Brattstrom (1953). Ecological studies of leopard lizards have been conducted in California (Montanucci, 1965, 1967), Colorado (McCoy, 1967), and Nevada (Turner et al., 1969; Tanner and Krogh, 1974a, 1974b).

## STUDY AREAS AND METHODS

This paper is based on 244 *C. wislizeni* (deposited at the Los Angeles County Museum of Natural History) collected on desert study areas scattered over much of the species' geographic range. Additional data from 11 specimens in the Arizona State University collection, and L. J. Vitt's personal collection are included. "Northern" specimens from the Great Basin Desert were collected at major sites in Idaho (I, 60 km S of Mountain Home), Nevada (Su, Sulfur; L, Lovelock; G, Gabbs; and V, Beatty), and Utah (U, 4 km W Grantsville). "Southern" specimens from the Sonoran, Mohave and Chihuahuan deserts were collected in Utah (Washington County), Nevada (P, Pahrump; S, Searchlight), California (M, Mojave; T, Twentynine Palms), Arizona (R, Salome; SM, South Mountain; and various localities in Maricopa, Cochise, Yuma, Pima, and Yavapai Counties), New Mexico (EP, southern Dona Ana County), and Sonora (A, 7 km E Estero de Tastiota) and Baja California in Mexico. On one area in Utah (U), 73 field-captured animals (plus 29 recaptures) and 95 laboratory hatchlings (9 recaptures) were marked and released to study growth rates, age at first breeding, movements, and survivorship. These lizards were processed in Salt Lake City and returned to the point of capture the next day. Each animal was sexed, weighed to the nearest 0.1 g, and measured for snout-vent (SVL) and tail length to the nearest millimeter. Distance between captures was estimated relative to local landmarks for short moves, and measured on an aerial photograph for longer distances. For all active *C. wislizeni* encountered above ground of their own volition, we recorded: date, time, approximate size, and microhabitat position when first sighted. Most animals on areas other than the above-mentioned Utah site were collected; these specimens provided additional data on cloacal temperature, sex, wet weight, exact size (SVL), and whether or not the tail had been broken and regenerated. All SVL and tail lengths were measured to the nearest

millimeter on live or freshly killed specimens before preservation. Dissection of preserved specimens supplied additional information on gonadal state and stomach contents. Testes lengths and widths of preserved specimens were measured with vernier calipers or metal millimeter rulers, and ratios of mean testis length over SVL were calculated. Some males were also checked for spermatozoa by crushing a section of the vas deferens. Ovigerous females (those with eggs in their oviducts) and their eggs were either weighed to the nearest 0.1 g or their volume was estimated by volumetric displacement (a nearly one-to-one correspondence between weight and volume indicated their equivalence). Volumes of intact stomachs were estimated similarly to the nearest 0.1 cm<sup>3</sup> with a small narrow-necked graduated cylinder. Both numbers and volumes of items in various prey categories were estimated for each stomach. Approximate volumes of individual prey items were estimated visually, by the proportion of the total stomach volume taken up by a given item. Prey items in each stomach were counted individually. Methods employed are discussed in greater detail by Pianka (1965, 1967, 1970, 1973), Parker (1972), and Pianka and Parker (1972, 1975a), which papers also describe the locations, climates, faunas and floras of most study areas.

## RESULTS AND DISCUSSION

*Time of Activity*

Leopard lizards are usually active during relatively warm portions of the day, beginning activity later than many smaller sympatric iguanids. Figure 1 shows the times of activity of *C. wislizeni* on four northern study areas (I, G, L, and U) in the Great Basin Desert, by month. During May and June, activity is most concentrated between 1100 and 1300 h, while during July and August peaks of activity are between 0800 and 1100 h. These data suggest bimodal activity periods in July and August (our collecting activity was not as in-

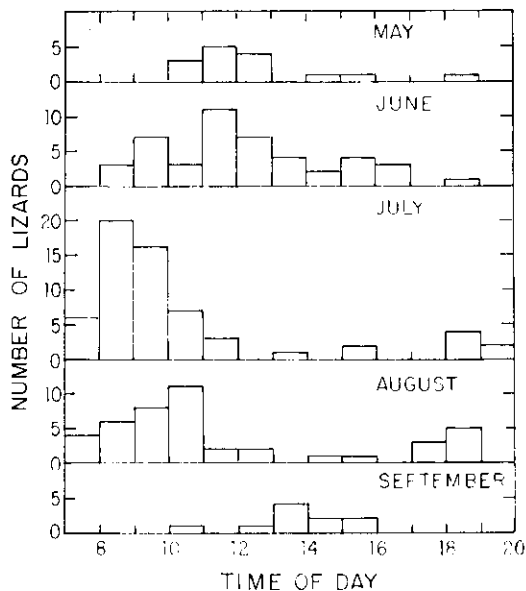


FIG. 1.—Frequency distributions of times of activity of *C. wislizeni* from four northern study sites (areas U, L, G, and I) showing seasonal changes in activity patterns.

tense after 1700 h as it was during the previous portion of the day), and unimodal periods in May, June, and September, with activity occurring throughout some days in June (however, without standardizing for diurnal variation in our own sampling effort, these trends are not conclusive). Similar seasonal trends in time of activity have been reported for many other lizard species (Mayhew, 1968; Pianka, 1969; and others). Expressing times of activity as “hours since sunrise” helps to standardize for such seasonal shifts in time of activity and facilitates comparisons between species (Pianka, 1973). The diversity of times of activity, or the “time niche breadth” of Pianka (1973), of southern *C. wislizeni* is the third broadest after *Phrynosoma platyrhinos* and *Sceloporus magister* among nine species of North American desert lizards (Pianka and Parker, 1975a). On northern study areas, however, *C. wislizeni* has a comparatively narrow time niche breadth (Table 1), indicating that activity is concentrated in a relatively brief period during the day com-

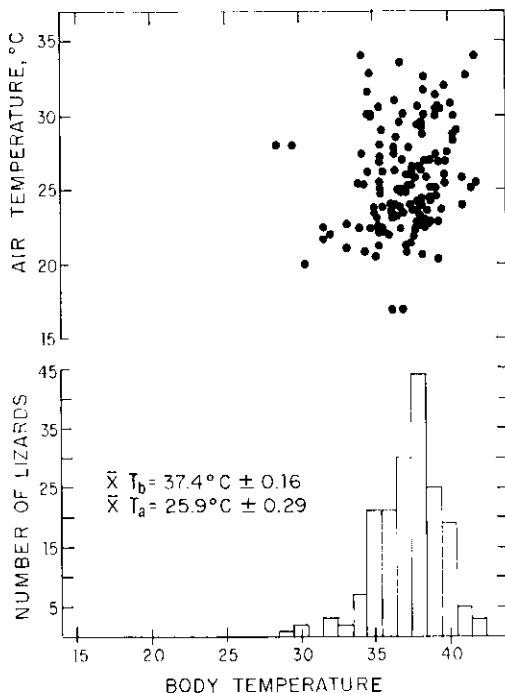


FIG. 2.—Body temperatures ( $T_b$ ) of active *C. wislizeni* plotted against ambient air temperature ( $T_a$ ). Frequency distributions of all active body temperatures ( $n = 183$ ; 144 northern, 39 southern) at the bottom of the figure.

pared to species such as *P. platyrhinos*, *Uta stansburiana*, and *Callisaurus draconoides*, which are active over a broader time span.

*Thermoregulation*

We obtained cloacal temperatures of 183 active *C. wislizeni*. There is a weak positive correlation ( $r = .24, p > .05$ ) between body temperature ( $T_b$ ) and ambient air temperature ( $T_a$ ) (Fig. 2). Our mean of  $37.4^\circ\text{C}$  ( $s = 2.2^\circ$ ) is somewhat lower than the means of  $38.7^\circ$  ( $N = 7$ ) and  $38.3^\circ$  ( $N = 19$ ) reported by Cowles and Bogert (1944) and Brattstrom (1965), respectively, for much smaller sample sizes. Means of  $37.34^\circ\text{C}$  for 144 northern lizards and  $37.39^\circ$  for 39 southern lizards were not significantly different ( $t$ -test,  $p > .90$ ). Body temperatures of active *C. wislizeni* are significantly more variable than  $T_b$  of four

TABLE 1.—Numbers of lizards active at different times of day in five diurnal species on five study areas in the Great Basin Desert. Diversity of time of activity is given at the far right.

SPECIES	HOURS SINCE SUNRISE															Diversity of time of activity	
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-		Total
<i>Cnemidophorus tigris</i>	3	27	78	105	39	16	6	5	1	1	2	1	2	2	1	289	4.24
<i>Uta stansburiana</i>	6	35	38	35	12	2	1	3	3	4	7	13	25	2	0	186	6.98
<i>Phrynosoma platyrhinos</i>	2	8	15	16	12	27	22	12	9	5	19	15	29	6	1	198	10.83
<i>Crotaphytus wislizeni</i>	1	17	34	26	17	6	2	2	1	2	3	4	7	0	0	122	5.87
<i>Callisaurus draconoides</i>	0	6	23	25	12	8	13	1	0	0	9	4	3	0	0	104	6.46
TOTALS	12	93	188	207	92	59	44	23	14	12	40	37	66	10	2	899	6.88 (mean)

of eight other sympatric lizard species (Pianka and Parker, 1975). *Crotaphytus wislizeni* is thus only slightly above average in  $T_b$  variance. Using methods similar to those of Licht et al. (1966), body temperatures of six recently captured (2 weeks) *C. wislizeni* were recorded at 4-min intervals over much of a daily period of activity on 6 consecutive days in a laboratory thermal gradient. Thus measured, the mean "preferred" body temperatures ( $T_b$ ) (preferred) of these six individuals varied from 35.9° to 37.5° C (overall  $\bar{x} = 36.8^\circ$ ,  $s = 1.97^\circ$ ,  $SE = .08^\circ$ ,  $N = 660$ ). Comparison of these  $T_b$  (preferred) statistics with those of active lizards under natural conditions shows that mean  $T_b$  is significantly higher than overall mean  $T_b$  (preferred) ( $t$ -test,  $p < .001$ ), whereas variances in  $T_b$  (preferred) and  $T_b$  do not differ significantly by an  $F$ -test. Means and/or variances of  $T_b$  (preferred) differ significantly from  $T_b$  in nature in most other species of lizards that have been examined (Licht et al., 1966; Pianka, 1971a, 1971b; Pianka and Parker, 1972, 1975a; Parker and Pianka, 1973; Pianka and Pianka, 1970, 1976). Using a cost-benefit argument, Huey and Slatkin (1975) argue that the optimal degree of thermo-

regulation that maximizes individual fitness will often be less in a thermally diverse natural environment than in a more homogeneous thermal gradient where the costs of regulating body temperature are lower.

#### Reproduction

Fitch (1970) summarized the literature on reproduction in *C. wislizeni*. The mean for 45 published clutch records, taken throughout the species' range, is 5.87, with study area means from 5.15 (Robison and Tanner, 1962) to 7.3 (McCoy, 1967). Pianka (1965) reported that clutch size may be larger in the south than in the north.

*Clutch Size and Reproductive Effort.*—We collected 94 gravid *C. wislizeni* during this study, of which 23 contained oviducal eggs, and 40 oviposited in the laboratory. Clutch size for 74 northern area clutches is strongly correlated ( $r = .62$ ,  $p < .01$ ) with female body size (Fig. 3), but in 20 southern clutches there was no significant correlation ( $r = .42$ ,  $p > .05$ ) perhaps because of small sample size and/or inclusion of clutch records from a large number of geographic areas. Mean clutch size varies considerably from area to area, and lati-

tudinal changes in clutch size are inconsistent (Table 2, Table 12). Some northern areas have particularly large clutches (area U,  $\bar{x}$  = 5.9; Colorado,  $\bar{x}$  = 7.3 [McCoy, 1967]), yet others in Idaho (I) and Nevada (L, G) have small clutches (Table 2). Clutch size distribution is unimodal, primarily because of the high mean on area U, where the mode is 6, versus a mode of 3 on other northern areas (Fig. 3). Weights (or volumes) of entire clutches of oviducal eggs, expressed as a percentage of total female weight (including the clutch), range from 9.5 to 27.2 on the various areas for preserved clutches, and show the same irregular trends as does mean clutch size. A similar reproductive effort (RE) for females from Utah ovipositing in the lab was calculated by using the weight difference between pre- and post-oviposition as the clutch weight, since eggs were not weighed. The resulting RE for 23 such clutches is significantly higher (*t*-test,  $p < .01$ ) than the RE for five preserved females and their eggs from the same locality (34.7 versus 25.2%). Expenditure per progeny (EPP), or weight of one egg over total female body weight, is also irregular, but northern lizards generally seem to lay larger eggs relative to their body weight than southern ones (Table 2). Among the 40 laboratory clutches, EPP is significantly negatively correlated with female SVL ( $r = -.75, p < .01$ ), and female weight ( $r = -.77, p < .01$ ). Actual egg weight was not significantly correlated with female SVL ( $r = .18, p > .05$ ). Individual egg weight thus appears to remain relatively constant regardless of size or age. Female SVL and weights were not significantly correlated with RE ( $r = .05$  and  $.11$ , respectively).

**Number of Clutches.**—Montanucci (1967) and Turner et al. (1969) found evidence for second clutches in leopard lizards from California and southern Nevada, respectively. We found no direct evidence for multiple clutches in any of our samples. The period over which gravid females were collected on northern areas spanned about

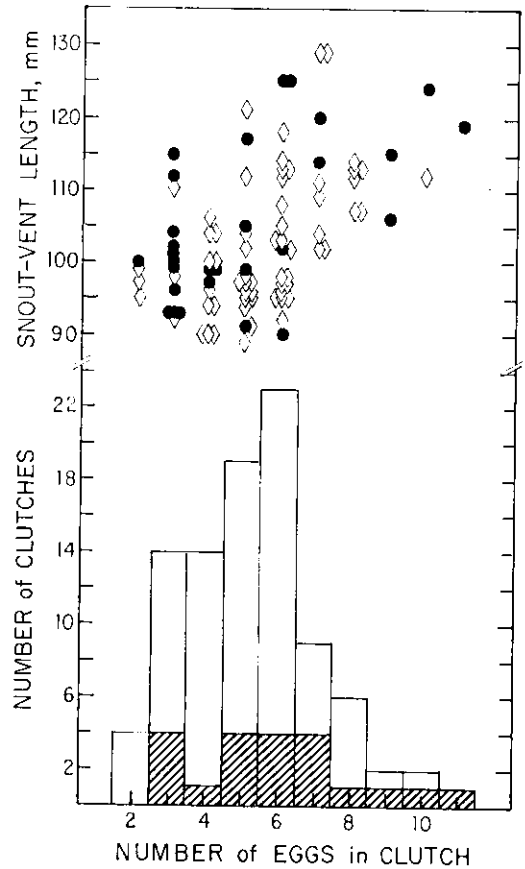


FIG. 3.—Plot of clutch size vs. snout-vent lengths of ♀♀, with frequency distribution of clutch sizes at bottom. Shaded areas = clutches from southern areas. Oviducal eggs and laid clutches depicted with open diamonds, yolked ovarian clutches by solid circles. One gravid ♀ was not measured.

1.5 months, compared to about 3 months on southern areas (Table 2), suggesting single broods on northern areas and multiple ones on at least some southern areas. Fitch (1970) found gravid females from Baja California over a 4-month period (March–June), further suggesting multiple clutches toward the south.

**Reproduction in Northern Utah (Area U).**—On area U, the reproductive seasons of 1971–1974 were followed. Females were gravid over only a relatively short period (Tables 2 and 3), with most ovigerous fe-

TABLE 2.—Snout-vent length (SVL), clutch size, reproductive effort (RE) and expenditure per progeny (EPP) data on adult *Crotaphytus wislizeni* ♀♀ from different geographic areas. Samples marked with asterisks include 40 laboratory clutches.

Area	Latitude	N	SVL (mm)		Clutch size		RE	EPP	N	Minimum dates of gravid ♀♀
			$\bar{x}$	range	$\bar{x}$	range				
Preserved clutches										
I	42° 25' N	7	98.1	93–104	3.43	3–4	12.2	2.93	2	15 June– 5 July
Su	40° 48' N	4	96.8	94–99	4.75	3–6	27.2	4.94	2	22–23 May
U	40° 36' N	52*	101.3	89–119	5.90	3–11	24.5	4.42	6	18 May–29 June
I.	40° 12' N	6	96.2	93–99	2.67	2–4	9.5	4.77	3	1 June–10 July
G	38° 48' N	5	100.0	98–102	3.60	2–6	14.7	2.94	1	5 June–6 July
Southern areas										
—	—	20	115.95	95–129	5.75	3–10	13.7	3.08	5	29 Apr–22 July
All northern areas										
—	—	74*	100.24	89–119	5.19	2–11	19.2	4.61	14	18 May–10 July
All areas										
—	—	94*	102.35	89–129	5.31	2–11	17.8	4.21	19	29 Apr–22 July
Laboratory clutches										
U-1972	40° 36'	10	103.4	90–119	6.50	4–10	34.7	5.34	10	—
U-1973		12	100.4	92–114	5.83	4–8	34.6	5.43	12	—
U-1974		18	100.9	89–114	5.44	3–8	35.0	6.88	18	—
U: 3 year total		40	101.5	89–119	5.83	3–10	34.8	6.08	40	—

males occurring in early June (19–29 June in 1971 and 9–28 June in 1972). Oviposition dates of 10 laboratory clutches laid in 1972 were 15 June (4), 17 June (1), 18 June (2), 19 June (2), and 30 June (1), indicating a very restricted period of oviposition. Similarly restricted periods were observed in 1973 and 1974: for 12 in 1973, 18 June (1), 19 June (6), 20 June (2), 22 June (1), 23 June (1), and 26 June (1); and for 18 in 1974, 14 June (3), 15 June (1), 16 June (3), 17 June (4), 18 June (2), 19 June (1), 20 June (2), 23 June (1), and 24 June (1).

A copulation was observed at 1605 h on 13 June 1971; both individuals were collected and the female contained ovarian oocytes 10 mm in diameter (presumably very close to ovulation). An attempted copulation was observed from 1334–1340 h on 19 June 1971, both were again collected, and the female was in the process of ovulating. One egg was in an oviduct, and five others averaging 8 mm in diameter had not yet ovulated. Females may be most receptive to males just before ovulation. This could insure presence of fresh spermatozoa in the oviducts before a shell is secreted around the egg. Follicular

atresia was observed in two females. A 98-mm female with six oviducal eggs had five atretic follicles, and a 102-mm female which had deposited six eggs in the laboratory had four atretic follicles. Clutch counts based solely on ovarian oocytes may thus be somewhat misleading.

Gravid females apparently made special trips for oviposition to an 850-m segment of an old, unused dirt road at area U (the source of laboratory clutches), where the sandy soil may have facilitated burrow construction. In 1973, individual gravid females were found over a short timespan as follows: 16 June (five gravid), 17 June (four gravid), 21 June (two gravid), 28 June (none), 3 July (one parturient), and 11 July (none). In 1974, captures were as follows: 28 May (none), 30 May (none), 9 June (three gravid), 11 June (10 gravid), 12 June (two gravid), 14 June (two gravid and one parturient), 25 June (none), 27 June (two parturient), 29 June (one parturient), and 5 July (two parturient). Two adult males first captured on 16 June 1973 were recaptured on 3 and 11 July 1973, but none of the 11 females were seen in the area, presumably having moved away soon after their release after oviposition. The sex

TABLE 3.—Snout-vent lengths (mm) of dissected gravid and nongravid *Crotaphytus wislizeni* ♀♀ from Utah (1971 + 1972).

Month	N	Gravid		Nongravid		Gravid (%)	Ovigerous (%)
		$\bar{x}$	range	$\bar{x}$	range		
May	3	105.3	91–119	—	—	100.0	0.0
Jun	21	101.4	90–113	103.7	97–112	85.7	76.2
Jul	3	—	—	99.0	92–105	0.0	0.0
Aug	3	—	—	94.0	92–95	0.0	0.0
Sep	1	—	—	97.0	—	0.0	0.0

ratios of 4:12 in 1973 and 8:19 in 1974 along this road also suggest special movements by females into the area, particularly since Montanucci (1965) and Turner et al. (1969) found sex ratios biased 2:1 in favor of males. Population density along this road (ca. 0.85 ha) was thus about 19 adults/ha during the oviposition period in 1973, a figure higher than maximum densities of 5/ha reported by Turner et al. (1969), further suggesting special migrations for oviposition temporarily increasing local population density.

Females captured in successive years returned to near their previous year's capture point to lay eggs again. Average distance between captures along the road for five gravid females captured in different years was 45 (35–60) m. One gravid female captured in 1974 had been released as a laboratory hatchling in 1972. It was captured 115 m from its 1972 release point.

Two egg-laying burrows on area U consisted of L-shaped tunnels about 20 cm long and 7–8 cm deep at their ends. Both were still under construction, however, as gravid females were found in them. Females apparently made numerous attempts at starting a burrow before actually finishing one, since signs of digging were evident along the old road during mid-June 1973.

Montanucci (1967) found that egg laying occurred between 1300–1700 h. Our data for seven females observed during oviposition show four between 1230–1700 h, two between 2130–2300 h, and one between 0845–1112 h.

Communal egg laying may occur in Utah

*C. wislizeni*. Three gravid females which oviposited in the laboratory (within 3 days of collection) were found in the same burrow entrance at 1110 and 1129 h on 12 June and at 1204 h on 14 June 1972. In 1973, three females were caught at the same spot on 17 and 21 June, two in burrows constructed at the same site on different days. Three colubrid snake species (*Coluber constrictor*, *Masticophis taeniatus*, and *Pituophis melanoleucus*) lay eggs communally in burrows on the same area (Parker and Brown, 1972; Parker, 1974), but, to our knowledge, communal nesting in a North American iguanid has never been reported. The tropical iguanid genus *Anolis* contains several species that nest communally (Rand, 1967), and *Iguana iguana* forms nesting aggregations (Rand, 1968). Members of the family Gekkonidae including *Gonatodes albogularis* (Sexton and Turner, 1971), *Hemidactylus mabouia* (Loveridge, 1923; Pendlebury, 1972), *Gekko gecko* (Gratz, 1973), *Ptyodactylus hasselquistii* (Werner, 1965), and *Gehyra variegata* (Bustard, 1968), lay communally, as do the teiids *Cnemidophorus sexlineatus* (Brown, 1956) and *Teius teyou* (Vaz-Ferreira et al., 1970) as well as the skink *Leiopeltis guichenoti* (Mitchell, 1959). Apparently communal nesting may sometimes be a result of a limited number of suitable nesting sites for the number of females present in the population.

A total of 32 gravid females from area U laid eggs in the laboratory (four twice and two, three times). Each female was weighed and then placed in a jar ( $\approx$  2 liters) containing 10 cm of moist earth

TABLE 4.—Data on ♀ size, egg weights, hatchling size, hatching success, incubation period and sex ratios for 40 clutches laid by *C. wislizeni* from Utah (area U) in the laboratory in 1972, 1973 and 1974. Eggs damaged during or after oviposition excluded from hatching success calculations. Egg weights = weight loss by female/clutch size. Means for egg weights and hatchling sizes are means of individual clutch means. Mean  $\pm 1$  SE, extremes in parentheses.

Year	♀♀		Eggs (N)	Clutch size	Egg wt (g)	Hatchlings				Hatch- ing success (%)	Incuba- tion period (days)	♂:♀ sex ratio
	N	SVL (mm)				N	SVL (mm)	Tail (mm)	Wt (g)			
1972	10	103.3 $\pm 2.39$ (90–113)	65	6.5 $\pm$ 0.52 (4–10)	2.27 $\pm$ 0.05 (1.98– 2.58)	42	42.9 $\pm$ 0.31 (38–46)	75.3 $\pm$ 1.06 (65–82)	2.5 $\pm$ .08 (1.8– 3.1)	73.7	47–54	—
1973	12	101.4 $\pm 1.90$ (94–114)	70	5.83 $\pm$ 0.37 (4–8)	2.15 $\pm$ 0.08 (1.75– 2.68)	61	43.7 $\pm$ 0.54 (39–48)	76.2 $\pm$ 1.57 (58–87)	2.7 $\pm$ .09 (2.1– 3.3)	89.7	43–45	31:30
1974	18	100.9 $\pm 1.95$ (89–114)	98	5.44 $\pm$ 0.33 (3–8)	2.41 $\pm$ 0.11 (1.90– 3.52)	31	41.9 $\pm$ 0.37 (39–45)	68.4 $\pm$ 0.73 (57–76)	2.6 $\pm$ .21 (2.3– 3.2)	31.6	57–61	19:12

from a snake oviposition site. Females were checked frequently during the day. When all eggs had been laid, females were removed and weighed again, then marked and released. Eggs were left undisturbed in the sealed jars, and incubated at 30° C. One clutch was completely destroyed by the female before her removal, and a few other eggs were similarly ruined. Nevertheless, hatching success among remaining eggs was high, 73.7% in 1972 and 89.7% in 1973 (Table 4). Snout-vent lengths, tail lengths, and weights of hatchlings varied considerably. Interestingly, average egg weight was significantly correlated with mean hatchling SVL ( $r = .44$ ,  $p < .05$ ), but not with hatchling weight ( $r = .14$ ,  $p > .05$ ). W. K. Derickson (unpublished data) demonstrated a positive correlation between calories/egg and hatchling size in *Sceloporus*. Among the 1972 hatchlings, 32.5% had tail abnormalities consisting of twisting and/or shortening of the distal portion of the tail. Such abnormalities were also seen in 2 of 39 (5.1%) adults from area U. Tail abnormalities may result from high temperature incubation of eggs (Bustard, 1969). Incubation periods were all similar, with only an 8-day range (47–54

days) in 1972, and 3 days (43–45) in 1973. Eggs were not incubated at a constant temperature in 1974. These incubation data compare to estimates of 32–34 days (Ruthven and Stuart, 1932), 35–49 days (McCoy, 1967), and 57 days (Montanucci, 1967) for *C. wislizeni*, and 52–94 days for *C. collaris* (Fitch, 1970).

No significant annual variations in clutch size were observed on area U. Variances in mean SVL of gravid females, clutch size, egg weight and hatchling weight between 1972, 1973, and 1974 were not significant ( $F$ -tests) (Table 4). Hatchling SVL and tail lengths, however, were significantly more variable between years ( $F$ -tests,  $p < .05$  for SVL;  $p < .01$  for tail lengths). The means for linear measurements of 1974 hatchlings were lower than in 1972 or 1973, perhaps a result of the irregular incubation temperatures to which eggs were subjected in 1974.

Four females laid eggs in 2 different years and two females laid eggs in 3 successive years (Table 5). Four exhibited decreases in clutch size, two laid clutches of the same size, and two showed increases. Decreases seemed partially correlated with age (females 1 and 2), but occurred in two



TABLE 5.—Records of weight, SVL, clutch size, egg weights, reproductive effort, and hatchling sizes in *Crotaphytus wislizeni* ♀♀ from Utah which oviposited in more than one year.

No.	Female SVL (mm)	Pre-oviposition wt (g)	Parturient wt	Oviposition date	Clutch size	RE	EPP	$\bar{x}$ egg wt (g)	$\bar{x}$ hatchling values	
									SVL (mm)	Wt (g)
1	112	53.2	32.0	18 Jun '72	10	39.9	3.9	2.12	43.8	2.6
	113	41.7	28.6	17 Jun '74	6	31.4	5.2	2.18	43.0	2.6
2	113	52.3	34.2	15 Jun '72	8	34.6	4.3	2.26	43.0	2.4
	114	49.7	33.9	22 Jun '73	8	31.8	3.9	1.98	43.7	2.9
	114	48.0	33.1	14 Jun '74	6	31.1	5.2	2.48	—	—
3	105	45.1	29.6	17 Jun '72	6	34.4	5.7	2.58	43.5	2.5
	112	45.1	29.0	19 Jun '73	6	35.7	5.9	2.68	47.7	3.3
	112	42.7	25.2	17 Jun '74	7	41.0	5.9	2.50	—	—
4	102	—	28.2	(1972)	—	—	—	—	—	—
	103	36.3	24.0	19 Jun '73	6	34.1	5.7	2.05	40.7	2.3
	104	39.2	25.5	16 Jun '74	5	34.9	6.9	2.74	—	—
5	103	39.8	26.4	20 Jun '73	6	33.8	5.6	2.23	43.4	2.6
	107	48.3	29.6	18 Jun '74	8	38.7	4.8	2.34	—	—
6	97	31.7	21.2	19 Jun '73	5	33.1	6.6	2.10	43.8	2.7
	100	35.0	22.2	18 Jun '74	4	36.6	9.1	3.20	—	—

younger females also (Nos. 4 and 6). Possibly 1974 was a particularly poor year, leading to clutch decreases in many females. Mean clutch size for all 1974 females was lower in 1974 than in 1972 or 1973, but the 1974 sample included more young females which lowered the average snout-vent length (Table 4). Similarly, no consistent patterns of increasing RE or EPP were observed in females ovipositing in different years (Table 5). Changes in RE were usually slight; three instances of decrease involved older females (Nos. 1 and 2). Patterns of EPP from year to year were irregular, but individual egg weights for several individuals (Nos. 1, 3, and 5) were similar in different years. Hatchling sizes also varied only slightly from year to year.

The 32 females that oviposited in the laboratory were assigned estimated ages on the basis of growth rates. Each individual was aged conservatively, i.e., as a slow-grower. Although some inaccuracies undoubtedly arise in such arbitrary aging, the age of each female should be accurate to within 1 year. Clutch size, RE, and EPP

were compared to estimated female age (Fig. 4). As expected, clutch size consistently increases directly with age as it does with SVL (Fig. 3), perhaps decreasing at the oldest ages of about 8 yr (sample sizes for this age are very small). The pattern for RE is somewhat different, with similar RE's at ages 2–6 yr, and slight decreases at 7 and 8 yr. EPP decreases consistently with age, as it does with SVL, apparently leveling off somewhat after age 5 yr. These data, especially for RE, differ from data on other reptiles such as *Carphophis vermis* (Clark, 1970), and from theoretical expectations which indicate that reproductive effort should usually increase with declining expectation of future offspring and increasing age (Gadgil and Bossert, 1970; Pianka and Parker, 1975b). Adult *Crotaphytus wislizeni* may have high enough survivorship that their residual reproductive value (expectation of future offspring) is relatively constant with age (see also below and Pianka and Parker, 1975b). Vitt (1974) found a positive correlation between the total number of calories invested in eggs and adult

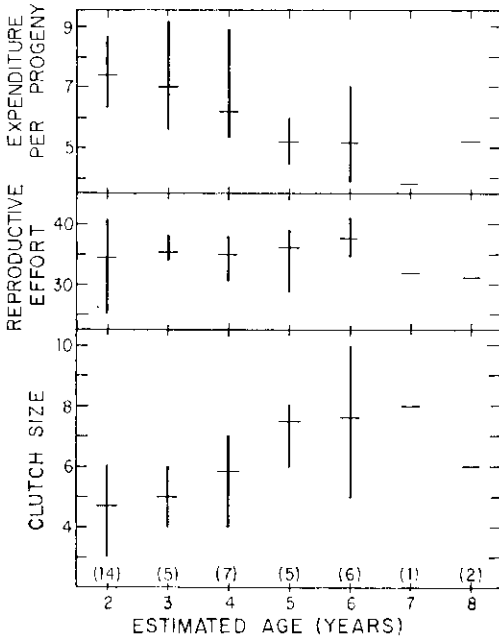


FIG. 4.—Age-specific changes of clutch size, reproductive effort (RE, total wet weight of eggs/total weight of gravid ♀), and expenditure per progeny (EPP, wet wt of one egg/total wt of gravid ♀) in 32 *Crotaphytus wislizeni* ♀♀ from 4 km W Grantsville, Utah, which oviposited in the laboratory. Horizontal lines = mean; vertical lines = range. Numbers in parentheses = sample size. Two ♀♀ are depicted three times and four ♀♀ twice at different ages.

size in the anguoid lizard *Gerrhonotus coeruleus*. If egg weight and calories invested in each egg are directly related as shown by Ballinger and Clark (1973), our data indicate that reproductive effort in *Crotaphytus wislizeni* from Utah does not increase with size or age.

**Hatching.**—At Phoenix South Mountain in Arizona, hatchlings (48–51 mm) were collected on 30 June and 8, 13, and 20 July 1966. In contrast, Utah hatchlings were first seen on 28 August 1971, and the above cited laboratory clutches hatched between 6–16 August 1972 and 31 July–9 August 1973. In southern California, eggs may hatch as early as 8 July (Montanucci, 1967), similar to Arizona. On northern areas, however, hatching is consistently later: early

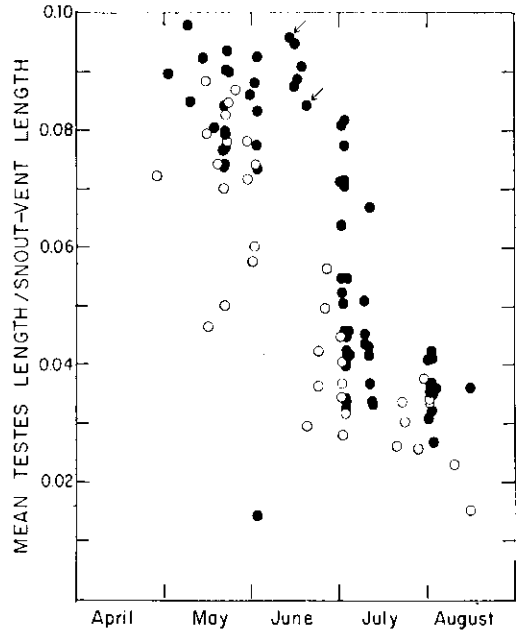


FIG. 5.—Seasonal changes in the ratio of  $\bar{x}$  testis length to SVL of *C. wislizeni* ♂♂ (84 mm and larger). Each dot is the mean ratio for both testes of a given ♂. Closed dots represent lizards from the Great Basin Desert; open dots are animals from the Chihuahuan, Mojave, and Sonoran Deserts. Arrows indicate copulating ♂♂.

August in Nevada and Utah (Ruthven and Stuart, 1932); 6–12 August in Colorado (McCoy, 1967).

**Testicular Cycles.**—Male testicular cycles closely parallel the female reproductive cycle. In the north, males emerge from hibernation in May with enlarged testes, a maximum is attained in late May or early June, decline begins in late June or early July, and complete regression is reached by August (Fig. 5). In the south, testes are also enlarged upon emergence in April or May, but regression begins sooner than in the north. Two general north-south patterns of testicular cycle difference thus occur in five lizard species we have studied. *Uta stansburiana* (Parker and Pianka, 1975) is similar to *C. wislizeni* with early regression in the south. In these two species, breeding season length for males is presumably similar through much of the range,

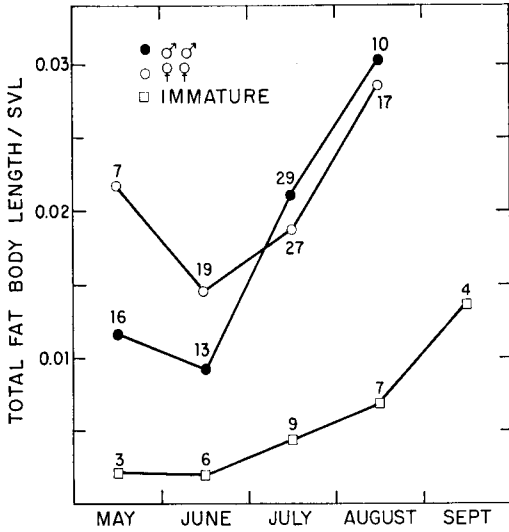


FIG. 6.—Seasonal changes in relative size of abdominal fat bodies in adult and immature *Crotaphytus wislizeni* from five northern areas (U, Su, L, G, N). Numbers indicate sample sizes.

and since southern animals become active earlier in the year, regression of testes starts sooner than in the north. Three other species, *Callisaurus draconoides* (Pianka and Parker, 1972), *Phrynosoma platyrhinos* (Pianka and Parker, 1975a), and *Cnemidophorus tigris* (Parker, 1973) show a reverse trend, with regression earlier in northern populations than in southern ones. For these three species, the male breeding season may thus be longer in the south; lizards emerge earlier in the year and have enlarged testes later into the summer.

*Fat Body Changes*

Samples of leopard lizards from five northern areas (combined) exhibited marked monthly changes in length of abdominal fat bodies (Fig. 6). Both adult males and adult females showed decreases from May to June, followed by an increase through August. The initial decrease in males was less marked than in females. Fat body depletion in the latter is apparently related to fat mobilization for oocyte growth in the ovary. Females with yolked ovarian

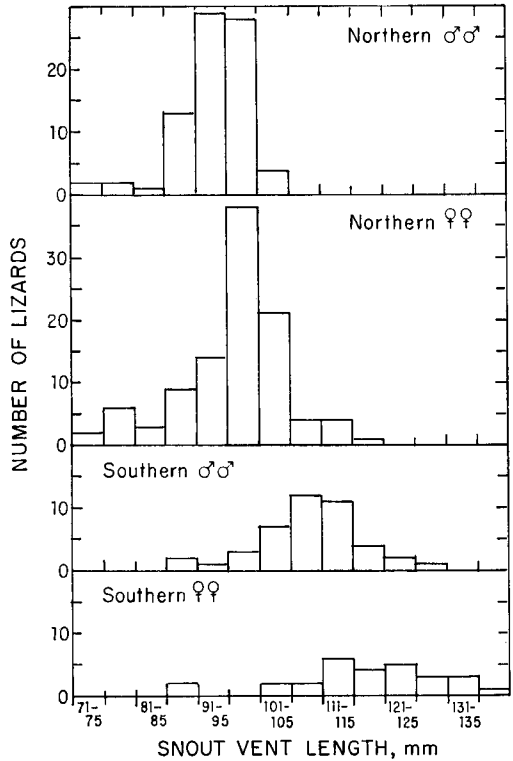


FIG. 7.—Frequency distributions of snout-vent lengths, by sex, in the Great Basin Desert (“northern”) and in the Mojave, Sonoran, and Chihuahuan Deserts (“southern”) showing increased size in the south. The figure includes all individuals > 70 mm SVL, thus including some sexually immature individuals of each sex.

oocytes had an average fat body index of 0.21 versus a mean of 0.13 for females with oviducal eggs, but the difference was not significant ( $t$ -test,  $.10 > p > .05$ ). Fat depletion in males between May and June could also be related to reproductive phenomena such as territorial defense (if it occurs) or searching for mates and courtship, activities perhaps requiring increased energy expenditure. Immatures showed no significant decrease from May to June, and marked increases as in adults during subsequent months. Absence of a decrease in immatures between May and June further suggests that adult decreases are related to reproductive activities.

TABLE 6.—Selected records of growth of juvenile *Crotaphytus wislizeni* from 4 km W Grantsville, Utah.

No. & Sex	Capture dates	SVL (mm)	Tail (mm)	Weight (g)	Remarks
1 ♂	24 Sep '71	62	116	7.4	
	31 May '73	88	175	16.4	
2	8 Aug '72	38	65	2.0	Hatched in laboratory
	27 Aug '73	79	166	15.2	
3	1 Aug '73	43	69	2.7	Hatched in laboratory
	27 Aug '73	51	89	3.8	
	12 Jun '74	69	130	8.5	
4 ♀	18 Sep '71	64	115	6.7	
	14 Jun '72	80	150	12.6	
5	6 Aug '72	44	80	2.5	Hatched in laboratory
	3 Sep '72	55	105	5.2	
6	14 Jun '72	78	—	13.1	
	4 Aug '72	95	186	25.2	
7	6 Aug '72	41	70	2.1	Hatched in laboratory Gravid
	14 Jun '74	89	—	26.3	
8	3 Aug '73	48	87	3.0	Hatched in laboratory
	29 Jun '74	84	165	17.2	
9	3 Aug '73	42	71	2.4	Hatched in laboratory
	11 Jun '74	74	150	11.5	

#### *Size, Growth, Age, and Survivorship*

In both northern and southern populations, *C. wislizeni* females attain larger sizes than males, but SVL in pooled samples from southern populations is significantly larger than from northern populations (*t*-test,  $p < .01$ ) (Fig. 7). Northern *C. wislizeni* are also much more abundant, having considerably higher population densities than southern ones. With about equal collecting effort on northern and southern areas, nearly three times as many individuals were collected in the north. Such abundance differences are probably related to occupancy of different trophic levels in north and south (see *Food Habits*).

Size at maturity is similar in both northern (84 mm) and southern (86 mm) males. Females, however, differ between north and south, with the smallest gravid northern female being 89 mm, and the smallest southern one 95 mm (Table 2).

Growth records from the northern area

U (Table 6, Nos. 6, 7, and 8) indicate that females reach minimal adult size in late summer at an age of  $\approx 1$  year, but breeding will obviously not occur until the following spring at an age of about 22 months. Males on area U may similarly not reach minimal adult size until late in their first full year (Table 6, No. 2). On the southern area SM, one juvenile presumably hatched in early July was 63 mm on 10 August 1966, and would thus possibly have grown enough to reach sexual maturity at  $< 1$  year old. Our data agree with other studies which show that northern *C. wislizeni* mature at age 2 (McCoy, 1967), while age at maturity may vary between 1–2 years in southern populations depending on favorable conditions for growth and other factors (Turner et al., 1969; Tanner and Krogh, 1974a).

Growth rates for periods during which leopard lizards were active were calculated assuming adult activity from May through

August and juvenile activity from April through September. Growth rate in three juveniles recaptured in the year of hatching was 0.35 mm/day (over an average time of 23 days). In juveniles recaptured for the first time during the summer after their first hibernation, the growth rate was 0.19 mm/day in two males (107–202 days), and 0.24 mm/day in four females (average of 104 days). Among three adult males, the rate was 0.04 mm/day (average 68 days), and among seven adult females, 0.02 mm/day (average 135 days). Two females first captured at one-year-old and recaptured the following summer averaged 0.08 mm/day (65–66 days). These data suggest that juvenile females grow slightly faster than juvenile males, but the pattern is reversed in adults.

Minimum adult survivorship between 1972 and 1973 in one small area at area U (Utah) was 50% for males (1 of 2) and 50% for females (5 of 10). The same male and four of the females were still alive in 1974. Minimum survivorship between 1973 and 1974 was 25% in males (1 of 4) and 46.7% in females (7 of 15). Turner et al. (1969) similarly found about 50% annual adult survivorship in southern Nevada populations of *C. wislizeni*.

Minimum survivorship in juveniles was distinctly lower than in adults. Among 34 laboratory hatchlings released in 1972, only one male was recaptured in 1973 and one female in 1974 (minimal 5.9% first year survivorship). Among 61 laboratory hatchlings released in 1973, at least 3 (1 ♂, 2 ♀♀) survived to 1974 (4.9%). These five hatchlings were from parents of five different ages (2–6 years), and the clutches from which they hatched had average RE's and EPP's which were at or below the average for all 40 clutches.

#### Life Table

A life table for *C. wislizeni* on area U was constructed using our survivorship and fecundity data from that area (Table 7). To obtain a table yielding a net reproductive rate ( $R_0$ ) of 1 (indicating a stable

TABLE 7.—Estimated age-specific survivorship and fecundity of *Crotaphytus wislizeni* on area U, 4 km W Grantsville, Utah, assuming a stable population size.  $l_x$  = survivorship to age  $x$ ;  $m_x$  = age-specific fecundity.

Age, $x$ (years)	$l_x$	$m_x$	$l_x m_x$
0	1.0000	0	
1	.4716	0	
2	.2130	2.4	.5112
3	.0962	2.5	.2405
4	.0435	3.0	.1305
5	.0196	3.4	.0666
6	.0088	3.75	.0330
7	.0040	4.0	.0160
8	.0018	3.0	.0054
			$R_0 = 1.0032$

population size), we multiplied survivorship ( $l_x$ ) by a factor of 11.2. The table shows the observed increase in age-specific fecundity ( $m_x$ ) through age 7 and the subsequent decrease at age 8 (see also Fig. 4). The life table indicates that the greatest contributions to fitness in terms of  $l_x m_x$  values are made by the youngest sexually mature age groups (ages 2 and 3). This agrees well with observed numbers of gravid females in each age group that were actually collected. Among the 40 gravid females on area U, 47.5% were 2 or 3 years old (Fig. 4). Thus, although age-specific fecundity increases with age, reduced survivorship in older age groups (4–7 years old) leads to a reduction of their contribution to  $l_x m_x$ . Age-specific expectation of future offspring, or residual reproductive value, is relatively flat with age during the peak years of reproduction (see also Pianka and Parker, 1975b). Compared to other lizard species, our tentative life table for *C. wislizeni* is most similar to the one for the late-maturing iguanid *Sceloporus graciosus* in southern Utah (Tinkle, 1973).

#### Movements

Some long-range dispersal of juvenile males is indicated by long movements of 806 m (14 days) and 1186 m (20 months). Four laboratory hatchlings recaptured rela-

TABLE 8.—Broken tail frequencies in *C. wislizeni* from northern and southern study areas.

Group	Sample size	Specimens with broken tails	
		N	%
Northern			
All individuals	196	11	5.6
All adults	161	10	6.2
Southern			
All individuals	71	8	11.3
All adults	65	8	12.3

tively soon after release (3–28 days) averaged moves of 100.5 (12–190) m, while four others (both sexes) recaptured after 9–22 months averaged 196 (115–300) m between capture points. Distances between captures of gravid females in successive years were given above. Movements of seven adult males over generally short periods (12–30 days) averaged 125 (0–450) m.

### Broken Tails

Frequencies of broken regenerated tails in *C. wislizeni* are relatively low, only slightly higher than in *Phrynosoma platyrhinos* (Pianka and Parker, 1975a). As in *Cnemidophorus tigris* (Pianka, 1970), *Uta stansburiana* (Parker and Pianka, 1975), *Callisaurus draconoides* (Pianka and Parker, 1972), and *P. platyrhinos*, broken tail frequencies of *C. wislizeni* are higher in southern populations (Table 8). Differences between north and south, while not statistically significant, suggest greater predation pressure in the south.

### Food Habits

On northern study areas, leopard lizards consume primarily grasshoppers, beetles, and small vertebrates (primarily other lizards), in order of volumetric importance (Table 9). Vertebrate prey in the north were usually other lizard species (*Calli-*

TABLE 9.—Summary of stomach contents of 181 *C. wislizeni* from five study areas (I, L, G, U, & V) in the Great Basin Desert. N = no. of food items in stomachs.

Food item	N	Volume (cm <sup>3</sup> )	% Total		Frequency in stomachs	
			N	Volume	N	%
Araneae	37	2.21	3.53	1.10	26	14.4
Scorpionidae	2	.50	.19	.25	2	1.1
Formicidae	38	1.38	3.63	.69	12	6.6
Other Hymenoptera	90	6.75	8.59	3.37	36	19.9
Locustidae	265	84.77	25.29	42.34	132	72.9
Blattidae	1	.20	.10	.10	1	.6
Mantidae	6	1.40	.57	.70	6	3.3
Coleoptera	298	37.15	28.44	18.56	111	61.3
Hemiptera	1	.03	.10	.01	1	.6
Diptera	51	7.20	4.87	3.60	35	19.3
Lepidoptera	6	5.50	.57	2.75	5	2.8
Insect eggs	26	1.10	2.48	.55	3	1.7
Insect larvae	45	5.60	4.29	2.80	30	16.6
Insect pupae	1	1.20	.10	.60	1	.6
Unidentified insects	78	5.54	7.44	2.77	53	29.3
Vertebrates	9	21.20	.86	10.59	12	6.6
Plants, floral	7	.60	.67	.30	2	1.1
Plants, vegetative	33	3.93	3.15	1.96	16	8.8
Unidentified material	54	13.95	5.15	6.97	69	38.1
TOTALS	1048	200.21				

TABLE 10.—Summary of stomach contents of 47 *C. wislizeni* from six study areas (P, S, T, R, SM, and A) in the Mojave and Sonoran Deserts. *N* = no. of food items in stomachs.

Food item	<i>N</i>	Volume (cm <sup>3</sup> )	% Total		Frequency in stomachs	
			<i>N</i>	Volume	<i>N</i>	%
Formicidae	12	.50	6.22	.29	2	4.3
Other Hymenoptera	8	.78	4.15	.46	4	8.5
Locustidae	32	12.70	16.58	7.47	20	42.6
Blattidae	1	.20	.52	.12	1	2.1
Mantidae	1	.10	.52	.06	1	2.1
Neuroptera	8	.80	4.15	.47	2	4.3
Coleoptera	42	3.25	21.76	1.91	16	34.0
Homoptera	4	.20	2.07	.12	1	2.1
Hemiptera	1	.01	.52	.01	1	2.1
Diptera	27	2.50	13.99	1.47	8	17.0
Insect larvae	25	2.45	12.95	1.44	6	12.8
Unidentified insects	9	.70	4.66	.41	6	12.8
Vertebrates	19	144.58	9.84	85.01	23	48.9
Plants, vegetative	3	.10	1.55	.06	1	2.1
Unidentified material	1	1.20	.52	.71	11	23.4
TOTALS	193	170.07				

*saurus draconoides*, *Cnemidophorus tigris*, and *Uta stansburiana*). On southern areas, other vertebrates were by far the most important prey items volumetrically, followed by grasshoppers (Table 10). As in the north, vertebrate prey of southern leopard lizards consisted mostly of lizards (the three species taken in the north plus *Phrynosoma* sp. and *Sceloporus* sp.). In its relations with sympatric lizard species, *C. wislizeni* thus appears to shift from a role as a predator on other lizard species (tertiary consumer) in the southern part of its range to that of a predator-competitor (secondary consumer) in the north (see also Fig. 11 in Pianka, 1970). Northern lizard species with

similar food habits are *Cnemidophorus tigris* (Pianka, 1970), *Phrynosoma douglassi* (Pianka and Parker, 1975a), and *Uta stansburiana* (Parker and Pianka, 1975). The larger size of southern *C. wislizeni* noted earlier may be an adaptation allowing utilization of a greater diversity of vertebrate prey and occupancy of a higher trophic level in the south, resulting perhaps from greater diffuse competition in the more diverse southern lizard communities.

Mean prey size was compared to mean head length of lizards in our samples (Table 11). Southern *C. wislizeni* have longer absolute head lengths and eat larger prey than northern ones. However, there

TABLE 11.—Correlations between head length and prey size in northern and southern populations of *Crotaphytus wislizeni*.  $r_1$  = head length categories versus mean volume of prey eaten by lizards with that head length;  $r_2$  = each lizard's head length versus the mean volume of its prey;  $r_3$  = prey size versus head length for all prey items. Significance levels: \* =  $p < .05$ ; \*\* =  $p < .01$ .

Area	<i>N</i>	Head length ( $\bar{x}$ )	Prey			$\bar{x}$ no. prey/ stomach		
			Size (cm <sup>3</sup> )	<i>N</i>	$r_1$		$r_2$	$r_3$
North	99	21.74	0.218	260	.176	.163	-.103	3.64
South	27	25.39	0.573	105	.246	.242	.201*	3.89
Combined	126	22.53	0.298	465	.253**	.197*	.123**	3.69

TABLE 12.—Major aspects of reproduction among four species of the lizard genus *Crotaphytus*.

Species and location	Clutch size		Period of oviposition	Max testes	Age at sexual maturity (yr)	Min SVL at maturity (mm)		Source
	$\bar{x}$	N				♂♂	♀♀	
<i>C. collaris</i>								
Kansas	5.76	33	Jun–Jul	—	1	88	77	Fitch (1956)
Western USA	6.7	47	—	—	—	—	—	Robison and Tanner (1962)
New Mexico	5.3	11	May–Jul	May	—	83	82	Parker (1973)
All records	6.19	91						
<i>C. reticulatus</i>								
Texas–Mexico	9.8	5	May–Jun	Apr–May	—	95	85	Montanucci (1971)
<i>C. silus</i>								
California	3	—	Jun–Jul	—	—	—	87	Montanucci (1965)
<i>C. wislizeni</i>								
Idaho	3.4	7	Jun–Jul	Jun–Jul	—	84	93	this paper
Utah	5.9	52	Jun	May	2	89	89	this paper
Nevada	3.5	15	Jun–Jul	May–Jun	—	86	93	this paper
Utah	5.15	21	—	—	—	—	—	Robison and Tanner (1962)
Colorado	7.3	10	Jul	—	2	81	95	McCoy (1967)
Nevada	5.8	15	—	—	—	—	—	Montanucci in Turner et al. (1969)
Nevada	6.47	19	Jun	May–Jun	2	—	—	Tanner and Krogh (1974a)
California	5.4	5	May–Jul	—	—	—	—	Fitch (1970)
Sonoran–Mojave–Chihuahuan Deserts	5.75	20	May–Jul	—	—	86	95	Montanucci (1967)
Baja California	—	—	Apr–Jun	—	—	—	—	this paper
All records	5.59	164						Fitch (1970)

was only one significant but weak correlation in several comparisons of head length and prey size within each geographic area. Correlations were consistently somewhat higher in the south (Table 11). Mean prey size in southern *C. wislizeni* was more than twice that of northern populations, reflecting the larger number of vertebrate prey taken in the south. The mean number of prey per stomach, however, was similar in both north and south.

#### Some Comparisons within the genus *Crotaphytus*

The genus *Crotaphytus* contains five species, *C. collaris*, *C. reticulatus*, *C. insularis*, *C. silus*, and *C. wislizeni*. *C. silus* was until recently considered a subspecies of *C.*

*wislizeni* (Montanucci, 1970). Little is known of the natural history of *C. insularis* (but see Axtell, 1972), thus we consider only the other four USA species here.

A number of ecological similarities and differences exist among these species of *Crotaphytus*. Reproductive aspects are summarized in Table 12. Similarities among the species include diets of large arthropods and small vertebrates, clutch size (*C. collaris* and *C. wislizeni*), testicular cycle, period of oviposition and size at maturity.

There are major differences as well. Sexual dimorphism in body size is present in three of the four species. There is little dimorphism in *C. silus*, but in *C. collaris* and *C. reticulatus* males are the larger sex, while in *C. wislizeni* females are larger.



These size differences could be related to a greater degree of male territoriality in *C. collaris*, *C. reticulatus* and *C. silus*. The only species in which females are larger than males (*C. wislizeni*) appears to lack territorial behavior (Montanucci, 1970, and others). In California, such territorial differences between *C. silus* and *C. wislizeni* may be related to habitat, with higher territoriality exhibited by *C. silus* in more open types of habitats (Montanucci, 1970).

*Crotaphytus wislizeni* is a late-maturing and single brooded species, in the sense of Tinkle (1969), at least in the northern part of its range, while *C. collaris* is an early-maturing multiple brooded species, even in northern parts of its range. *Crotaphytus silus* too is probably early-maturing and multiple brooded (Montanucci, 1965), but with a smaller clutch size than the other three species. *Crotaphytus reticulatus* is like both *C. collaris* and *C. silus* in producing multiple clutches, but its clutch size is larger than in the other species. Interspecific differences in sexual dimorphism could be related to reproductive patterns in each species: *C. collaris*, *C. reticulatus* and *C. silus* may have undergone selection for early maturity at smaller body sizes and multiple clutches (relatively *r*-selected); the opposite type of selection (for late maturity) may have occurred in *C. wislizeni* females, leading to a larger body size and comparatively *K*-selected populations, at least in the north.

Another major difference between the species is in the habitats they occupy. *Crotaphytus reticulatus* is found over a restricted geographic range in habitats of thorn bush desert (Montanucci, 1971, 1974). *Crotaphytus silus* is even more restricted in the San Joaquin Valley of southern California (Montanucci, 1965). The other two species have larger and more broadly overlapping geographic distributions, and the habitats they occupy are correspondingly more divergent, with *C. collaris* being primarily a rock-dweller (saxicolous) and *C. wislizeni* an essentially flatland desert form. In a preliminary study of the interrelations

of *C. collaris* and *C. wislizeni* where they are syntopic in Nevada, Snyder (1972) found considerable overlap in habitat distribution especially during spring mating. Generally, however, *C. collaris* was most frequently captured on steeper slopes (30%) with about 20% exposed substrate and 52% exposed rock outcroppings and boulders. In contrast, *C. wislizeni* was usually encountered on gentle slopes (~5%) with 69% exposed substrate and only 4% rock outcroppings. A further study of this nature, including detailed analysis of food habits, would be of interest.

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#### LITERATURE CITED

- ATNATT, S. R. 1939. Color changes as controlled by temperature and light in the lizards of the desert regions of southern California. Publ. Univ. California Los Angeles, Biol. Sci. 1:237-276.
- AXTELL, R. W. 1972. Hybridization between western collared lizards with a proposed taxonomic rearrangement. *Copeia* 1972:707-727.
- BALLINGER, R. E., AND D. R. CLARK, JR. 1973. Energy content of lizard eggs and the measurement of reproductive effort. *J. Herpetol.* 7: 129-132.
- BANTA, B. H. 1962a. A preliminary account of the herpetofauna of the Saline Valley Hydrographic Basin, Inyo County, California. *Wasmann J. Biol.* 20:161-251.
- . 1962b. Preliminary remarks upon the zoogeography of the lizards inhabiting the Great Basin of the western United States. *Wasmann J. Biol.* 20:253-287.

- . 1967. Some miscellaneous remarks on recent Nevada lizards. *Occas. Pap. Biol. Soc. Nevada* (16):1-5.
- BENTLEY, G. H. 1919. Reptiles collected in the vicinity of Currant, Nye County, Nevada. *Copeia* 1919 (75):87-91.
- BRATTSTROM, B. H. 1953. Pleistocene reptiles from California. *Copeia* 1953:174-179.
- . 1965. Body temperatures of reptiles. *Am. Midl. Nat.* 73:376-422.
- BROWN, E. E. 1956. Nests and young of the six-lined racerunner, *Cnemidophorus sexlineatus* Linnaeus. *J. Elisha Mitchell Sci. Soc.* 72:30-40.
- BUSTARD, H. R. 1968. The ecology of the Australian gecko, *Gehyra variegata* in northern New South Wales. *J. Zool. London* 154:113-138.
- . 1969. Tail abnormalities in reptiles resulting from high temperature egg incubation. *Brit. J. Herpetol.* 4:121-123.
- CAMP, C. L. 1916. Notes on the local distribution and habits of the amphibians and reptiles of southeastern California in the vicinity of the Turtle Mountains. *Univ. California Publ. Zool.* 12:503-544.
- CLARK, D. R., JR. 1970. Age specific "reproductive effort" in the worm snake *Carphophis vermis* (Kennicott). *Trans. Kansas Acad. Sci.* 73:20-24.
- COWLES, R. B. 1941. Observations on the winter activities of desert reptiles. *Ecology* 22:125-140.
- , AND C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* 83:265-296.
- CUNNINGHAM, J. D. 1966. Additional observations on the body temperatures of reptiles. *Herpetologica* 22:184-189.
- FAUTIN, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. *Ecol. Monogr.* 16:251-310.
- FITCH, H. S. 1956. An ecological study of the collared lizard, *Crotaphytus collaris*. *Univ. Kansas Publ. Mus. Nat. Hist.* 8:213-274.
- . 1970. Reproductive cycles in lizards and snakes. *Misc. Publ. Univ. Kansas Mus. Nat. Hist.* (52):1-247.
- GADGIL, M., AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1-24.
- GATES, C. O. 1957. A study of the herpetofauna in the vicinity of Wickenburg, Maricopa County, Arizona. *Trans. Kansas Acad. Sci.* 60:403-418.
- GRATZ, R. K. 1973. Life history: *Gekko gekko*. *HISS NEWS-J.* 1:91.
- HORTON, N. 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. *Am. Midl. Nat.* 53:88-114.
- HUEY, R. B., AND M. SLATKIN. 1975. A cost-benefit model of lizard thermoregulation. *Q. Rev. Biol.* (In press).
- JOHNSON, D. H., M. D. BRYANT, AND A. H. MILLER. 1948. Vertebrate animals of the Providence Mountains area of California. *Univ. California Publ. Zool.* 48: 221-376.
- JORGENSEN, C. D., AND A. M. ORTON. 1962. Note of lizards feeding on oatmeal bait. *Herpetologica* 17:278.
- JORGENSEN, C. D., AND W. W. TANNER. 1963. Voice of the leopard lizard *Crotaphytus wislizeni* Baird and Girard. *Proc. Utah Acad. Sci. Arts Lett.* 40:115-116.
- KLAUBER, L. M. 1939. Studies of reptile life in the arid southwest. *Bull. Zool. Soc. San Diego* 14:1-100.
- KNOWLTON, G. F. 1934. Lizards as a factor in the control of range insects. *J. Econ. Entomol.* 27:998-1004.
- . 1938. Lizards in insect control. *Ohio J. Sci.* 38:235-238.
- . 1948. Vertebrate animals feeding on the Mormon cricket. *Am. Midl. Nat.* 39:137-138.
- . 1974. Arthropod food of Curlew Valley lizards. *Utah State Univ. Ecol. Center Terrest. Arthropod Ser.* 7:1-7.
- , AND M. J. JANES. 1932. Studies of the food habits of Utah lizards. *Ohio J. Sci.* 32:467-470.
- . 1934. Distributional and food habit notes on Utah lizards. *Copeia* 1934:10-14.
- KNOWLTON, G. F., AND W. L. THOMAS. 1934a. Notes on some insectivorous Utah lizards. *Proc. Utah Acad. Sci. Arts Lett.* 11:257-259.
- . 1934b. Insect food of Trout Creek lizards. *Proc. Utah Acad. Sci. Arts Lett.* 12:263-264.
- . 1936. Food habits of Skull Valley lizards. *Copeia* 1936:64-66.
- 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.
- LINSDALE, J. M. 1938. Environmental responses of vertebrates in the Great Basin. *Am. Midl. Nat.* 19:1-206.
- LOVERIDGE, A. 1923. Notes on East African lizards collected during 1920-1923, with the description of two new races of *Agama lionotus* Blgr. *Proc. Zool. Soc. London* 1923:1937-1939.
- MAYHEW, W. W. 1968. Biology of desert amphibians and reptiles, p. 195-356. In G. W. Brown, Jr. [ed.] *Desert biology*. Academic Press, New York.
- MCCOY, C. J. 1967. Natural history notes on *Crotaphytus wislizeni* (Reptilia: Iguanidae). *Am. Midl. Nat.* 77:138-146.
- MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. *Univ. California Press, Berkeley.*
- MILSTEAD, W. W., AND D. W. TINKLE. 1969. Interrelationships of feeding habits in a popula-

- tion of lizards in southwestern Texas. *Am. Midl. Nat.* 81:491-499.
- MITCHELL, F. J. 1959. Communal egg-laying in the lizard *Leiopisma guichenoti* (Dumeril and Bibron). *Trans. R. Soc. South Australia* 82:121-122.
- MONTANUCCI, R. R. 1965. Observations on the San Joaquin leopard lizard, *Crotaphytus wislizenii* silus Stejneger. *Herpetologica* 21:270-283.
- . 1967. Further studies on leopard lizards, *Crotaphytus wislizenii*. *Herpetologica* 23:119-126.
- . 1970. Analysis of hybridization between *Crotaphytus wislizenii* and *Crotaphytus silus* (Sauria: Iguanidae) in California. *Copeia* 1970:104-123.
- . 1971. Ecological and distributional data on *Crotaphytus reticulatus* (Sauria: Iguanidae). *Herpetologica* 27:183-197.
- . 1974. Convergence, polymorphism or introgressive hybridization? An analysis of interaction between *Crotaphytus collaris* and *C. reticulatus* (Sauria: Iguanidae). *Copeia* 1974:87-101.
- ORTENBURGER, A. I., AND R. D. ORTENBURGER. 1926. Field observations on some amphibians and reptiles of Pima County, Arizona. *Proc. Oklahoma Acad. Sci.* 6:101-121.
- PACK, H. J. 1922. Food habits of *Crotaphytus wislizenii* Baird and Girard. *Proc. Biol. Soc. Washington* 35:1-4.
- PARKER, W. S. 1972. Aspects of the ecology of a Sonoran Desert population of the western banded gecko, *Coleonyx variegatus* (Sauria, Eublepharinae). *Am. Midl. Nat.* 88:209-224.
- . 1973. Notes on reproduction of some lizards from Arizona, New Mexico, Texas, and Utah. *Herpetologica* 29:258-264.
- . 1974. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* (Halliwell) and *Pituophis melanoleucus deserticola* Stejneger, in northern Utah. Ph.D. thesis, Univ. Utah, Salt Lake City. 295 p.
- PARKER, W. S., AND W. S. BROWN. 1972. Telemetric study of movements and oviposition of two female *Masticophis t. taeniatus*. *Copeia* 1972:892-895.
- PARKER, W. S., AND E. R. PIANKA. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. *Herpetologica* 29:143-152.
- . 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. *Copeia* 1975:615-632.
- PENDLEBURY, G. B. 1972. Nesting sites, eggs and young of *Hemidactylus mabouia* from Carriacou, West Indies. *Herpetol. Rev.* 4:203.
- PIANKA, E. R. 1965. Species diversity and ecology of flatland desert lizards in western North America. Ph.D. thesis, Univ. Washington, Seattle. 212 p.
- . 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47:1055-1057.
- . 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* 51:703-720.
- . 1971a. Comparative ecology of two lizards. *Copeia* 1971:129-138.
- . 1971b. Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. *Copeia* 1971:527-536.
- . 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4:53-74.
- PIANKA, E. R., AND W. S. PARKER. 1972. Ecology of the iguanid lizard *Callisaurus draconoides*. *Copeia* 1972:493-508.
- . 1975a. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia* 1975:141-162.
- . 1975b. Age-specific reproductive tactics. *Am. Nat.* 109:453-464.
- PIANKA, E. R., AND H. D. PIANKA. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in western Australia. *Copeia* 1970:90-103.
- . 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* 1976 (In press).
- RAND, A. S. 1967. Communal egg laying in anoline lizards. *Herpetologica* 23:227-230.
- . 1968. A nesting aggregation of iguanas. *Copeia* 1968:552-561.
- RICHARDSON, C. H. 1915. Reptiles of northwestern Nevada and adjacent territory. *Proc. U. S. Natl. Mus.* 48:403-435.
- ROBISON, W. G., AND W. W. TANNER. 1962. A comparative study of the species of the genus *Crotaphytus* Holbrook (Iguanidae). *Brigham Young Univ. Sci. Bull.* 2:1-31.
- RUTHVEN, A. G., AND L. C. STUART. 1932. Notes on the period of postdepositional development in several common lizards. *Occas. Pap. Mus. Zool. Univ. Michigan* (241):1-3.
- SEXTON, O. J., AND O. TURNER. 1971. The reproductive cycle of a neotropical lizard. *Ecology* 52:159-164.
- SHAW, C. E. 1952. Notes on the eggs and young of some United States and Mexican lizards. *I. Herpetologica* 8:71-79.
- SMITH, H. M. 1946. *Handbook of lizards. Lizards of the United States and Canada.* Comstock Publ. Co., Ithaca, New York.
- SNYDER, J. D. 1972. An ecological investigation of sympatric populations of the lizards *Crotaphytus collaris* and *C. wislizenii*. M.A. thesis, San Francisco State Univ. 88 p.



- STEBBINS, R. C. 1954. Amphibians and reptiles of western North America. McGraw-Hill Book Co., New York.
- STUART, L. C. 1932. The lizards of the middle Pahvant Valley, Utah: materials for a study in saurian distribution. Occas. Pap. Mus. Zool. Univ. Michigan (244):1-33.
- TANNER, W. W., AND J. E. KROGH. 1974a. Ecology of the leopard lizard, *Crotaphytus wislizeni*, at the Nevada Test Site, Nye County, Nevada. *Herpetologica* 30:63-72.
- . 1974b. Variations in activity as seen in four sympatric lizard species of southern Nevada. *Herpetologica* 30:303-308.
- TINKLE, D. W. 1959. Observations on the lizards *Cnemidophorus tigris*, *Cnemidophorus tessellatus*, and *Crotaphytus wislizeni*. *Southwest. Nat.* 4:195-200.
- . 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Am. Nat.* 103:501-516.
- . 1973. A population analysis of the sagebrush lizard, *Sceloporus graciosus* in southern Utah. *Copeia* 1973:284-296.
- TURNER, F. B., J. R. LANNOM, P. A. MEDICA, AND G. A. HODDENBACH. 1969. Density and composition of fenced populations of leopard lizards (*Crotaphytus wislizenii*) in southern Nevada. *Herpetologica* 25:247-257.
- VAZ-FERREIRA, R., L. C. DE ZOLESSI, AND F. ACHAVÁL. 1970. Oviposición y desarrollo de ofidios y lacertilios en hormigueros de *Acromyrmex*. *Physis* 29:431-459.
- VITT, L. J. 1974. Reproductive effort and energy comparisons of adults, eggs, and neonates of *Gerrhonotus coeruleus principis*. *J. Herpetol.* 8:165-168.
- WERNER, Y. L. 1965. Über die Israelischen Geckos der Gattung *Ptyodactylus* und ihre Biologie. *Salamandra* 1:15-25.
- WEVER, E. G., M. C. HEPP-REYMOND, AND J. A. VERNON. 1966. Vocalization and hearing in the leopard lizard. *Proc. Natl. Acad. Sci.* 55:98-106.
- WOODBURY, A. M. 1959. Clasp behavior of the leopard lizard. *Herpetologica* 15:118.

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