THE ECOLOGY AND SOCIAL BEHAVIOR OF THE CHUCKWALLA, *SAUROMALUS OBESUS OBESUS* BAIRD

BY

KRISTIN H. BERRY

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THE ECOLOGY AND SOCIAL BEHAVIOR OF THE CHUCKWALLA (*SAUROMALUS OBESUS OBESUS* BAIRD)

BY

KRISTIN H. BERRY

(A contribution from the Museum of Vertebrate Zoology of the University of California, Berkeley)

INTRODUCTION

THE CHUCKWALLA, *Sauromalus obesus,* is a large, rock-dwelling, herbivorous, iguanid lizard found in the Great Basin, Mojave, Colorado and Sonoran deserts of North America (Stebbins, 1966). Its desert habitat is characterized by extremes in temperatures and little available water for plant growth. Rainfall is scarce and erratic. Wildflowers produce few fresh shoots or blossoms unless winter rainfall reaches or exceeds the annual average.

Chuckwallas live in an environment that is rigorous and unpredictable, especially for an herbivore. Adaptive strategies for a harsh environment entail structural, behavioral, and physiological adaptations. In order to study the adaptive strategy of the chuckwalla and how it copes with the desert, a natural population of the chuckwalla, *Sauromalus obesus obesus* Baird, was intensively observed in the southern Great Basin from 1968 through 1971.

HABITAT

The study area lies at Lone Butte, a southwestern outcrop of the Argus Range, in San Bernardino County, California. Lone Butte is within the Naval Weapons Center at China Lake, and access to the public is restricted. The study site is a natural area untouched by the man for over 30 years.

Two east-west ridges form the backbone of the irregularly shaped 15 ha plot. The sandy desert floor of Salt Wells Valley lies to the south and east, forming a natural boundary. The rock ridges continue to the north and west, so an arbitrary line sets the limits of the study area in these directions.

Dark brown, exfoliating granitic outcrops are scattered over ridge tops, hillsides and in gullies. The decaying granite has formed a ground cover of small, sharp-edged rocks and on some hillsides there is loose talus.

The flora is typical creosote bush scrub plant community (Munz, 1959), composed predominantly of creosote bush (*Larrea divaricata*), burroweed (*Ambrosia dumosa*), and Fremont dalea (*Dalea Fremontii*). Brittle bush (*Encelia farinosa*), desert straw (*Stephanomeria pauciflora*), Mojave aster (*Machaeranthera tortifolia*) and bedstraw (*Galium stellatum* ssp. *eremicum*) grow in crevices of rock outcrops.

CLIMATE

The Argus Range is part of the Basin-Range Province (Great Basin) and is considered high desert (Jahns, 1954). The climate of high desert is characterized by extremes. Temperatures have been recorded in excess of 45°C in summer and below –12° C in winter. Precipitation occurs primarily in winter months between

October and March but is erratic. The amount of precipitation in winter determines annual and perennial flower production in spring.

Winter rainfall is very important to life in this desert and appears to affect almost every facet of a chuckwalla population. Growth, daily and seasonal activity, courtship, reproduction and aggression are dependent on adequate food supply and thus on rain. Since precipitation is a critical factor, patterns in the Argus and surrounding areas will be discussed in detail.

The average annual precipitation for this area, 7.37 cm, is based on records from 1946 to the present (U. S. Naval Weapons Center, 1971). From 1942 through 1956 the southwestern United States suffered a severe drought; southern California (and Lone Butte) received 50 to 85% or less of the average annual rainfall for several years during the 12 year drought period (Thomas, 1962; Troxell, 1957; U. S. Dept. Interior, 1951). A drought of this magnitude has occurred only 8 times since the 13th century. There have been 3 intensive dry periods in the last century alone: 1894–1904, 1928–1934, and 1942–1956 (Schulman, 1945; Schulman, 1947; Thomas, 1962; Troxell, 1957).

Precipitation during the drought in the Argus Range (1946–1957) averaged 5.45 cm, whereas the postdrought annual mean (1957–1970) was 8.26 cm. The latter figure is considered the typical annual mean for this area. During the four year study, winter rainfall varied from a low of 4.62 cm in 1970 to 12.3 cm in 1969. Below average rainfall occurs every two to three years.

No measurements were taken of the number of annuals/m^2 or flower production in the perennials during the study. However 1968, 1969, and 1971 were considered "moderate" to "good" wildflower years. Annuals covered the ground from March through May and perennials bloomed through June. 1970 was a "poor" year. The few annuals that occurred bloomed in the shade in rock crevices and under creosote bushes. Perennial shrubs produced few flowers and were dry by late June. Other parts of the desert experienced low rainfall in 1970. Nagy (1972, 1973) reported extremely dry conditions in the northern Mojave. Stebbins (personal communication) found leafless and flowerless shrubs and emaciated lizards at Pisgah Crater (San Bernardino County, California).

In the winter of 1970–1971, 6.17 cm of rain fell. Although slightly below the postdrought mean, annual wildflowers carpeted the slopes and gullies between and within rockpiles from February through May.

MATERIALS AND METHODS

The project began in March 1968 on a casual basis, as another program was underway. From ten to fifteen days per month were spent in the study area in July and August of 1969, April through August of 1970 and March through August in 1971. During spring, observations usually started at 9:00 to 10:00 A.M. and continued until 4:00 or 5:00 P.M. In summer, observations began at 6:00 to 8:00 A.M. and terminated at 10:00 to 11:00 A.M., depending on when chuckwallas retreated to crevices. In late summer several trips were made to the site in late afternoon and evening. Chuckwallas were observed for at least 600 hours in the field in 1969, 1970, and 1971. An additional 200 hours were spent in waiting for lizards to emerge and in capturing and marking lizards.

Lizards were captured, marked, and released from 1968 through 1971. To facilitate capture, 50 five-gallon cans with masonite lids were sunk to a depth level with the soil surface (Banta, 1957). These were placed 20 to 40 m apart in a pattern consistent with the ridge and outcrop topography. Seven east-west rows of varying numbers of cans covered approximately 60% of the area. A fish pole was used for noosing lizards. When a lizard retreated to a crevice, a dark cloth was placed over the opening; the fish pole was used to move the lizard toward the cloth where it could be captured. On rare occasions a hydraulic jack was used to temporarily spread a crevice. Rock crevices were left intact and were not shifted or damaged with a crowbar.

Each chuckwalla captured at Lone Butte was sexed, measured for snout-vent (SV) and tail lengths (VT), checked for parasites and general condition, and toe clipped. Females were palpated for eggs. Numbers were painted on the sides and on the left tail base with yellow ochre acrylic paint that harmonized with colors in the environment. These proved easy to identify at distances to 300 m. Not all chuckwallas observed could be captured. Uncaptured animals who could be recognized repeatedly were given names or letters instead of numbers.

Observations were made from 3 shelters. Chuckwallas and other animals were watched with 7 × 50 binoculars and a Questar telescope with 40, 80, and 160 power. Observations and identification were usually made at 80 power.

Movements and locations of lizards were plotted on aerial photographs of the study site. Sizes of territories and home ranges were calculated with a K & E compensating polar planimeter.

The following data were recorded for each animal: time of day and period of observations; behavioral activities (displays, feeding, courtship, etc.); location; movement; associations with other lizards and animals; temperatures 1 m and 1–2 cm above the substratum and on the substratum; and general weather conditions. Temperatures were measured with a Schultheis thermometer. During 1970 and 1971 a National Bureau of Standards Hygrothermograph continuously monitored air temperatures and humidity. All times mentioned are in Pacific Standard Time.

To supplement field studies, several chuckwallas were maintained in an outdoor pen 4.9 m wide × 6.7 m long × 2.4 m high covered with chicken wire. Basalt boulders littered the ground. The captive chuckwallas were fed romaine and dandelions, as well as desert annual wildflowers and perennial shrubs. The behavior of these lizards was compared with that of animals in the field.

POPULATION DYNAMICS

During the four year study, 116 chuckwallas were marked. Forty-two new individuals were captured in 1968, 25 in 1969, 35 in 1970 and 14 in 1971. The number and percentage of recaptures for each year are shown in table 1. Between 35.7 and 42.8% of the lizards captured in 1968 were recaptured in 1969, 1970 and 1971. Seventy-six and 75.6% of the 1969 animals were found in 1970 and 1971. The lizards recaptured in 1969, 1970, and 1971 represented 42.8%, 53.7% and 55.8% of the totals, respectively.

Mark and recapture data were used to estimate growth rates and to determine sex ratios, age structure, density and distribution of the population.

TABLE 1
MARK AND RECAPTURE DATA ON CHUCKWALLAS AT LONE BUTTE

	1968	1969	1970	1971
New individuals				
Males	24	12	22	9
Females	17	11	10	4
Juveniles	1(♂)	2(♀)	5(3♂s)	1*
Total	42	25	37	14
Percent recaptures				
1968		42.8	40.5	35.7
Male:Female		12:6	10:7	8:7
1969			76.0	75.6
Male:Female			10:9	11:7
1970				69.5
Male:Female (+ juvenile)				18:7
Total recaptures (%)	0	42.8%	53.7%	55.8%
Total lizards captured	42	43	73	72

* Captured in October 1971.

GROWTH AND AGE

Growth and aging of chuckwallas has been a subject of speculation. Johnson (1965) cited growth records for 19 individuals that ranged from 0 to 10 mm per year. One exceptional animal grew 15 mm. Johnson estimated a 25 year life span for a 200 mm SV animal. Schallenberger (1970) calculated age on the basis of growth rings on the dentary and zygapophyses, using a technique devised by Peabody (1961) and Warren (1963). There has been little evidence that growth rings correspond with actual age of the animal. Schallenberger's analysis and growth curve indicated a 200 mm adult to be 15 years old.

Charles Shaw (Johnson, 1965) and Mayhew (1963) reported growth rates for captive animals. These were kept under conditions of constant food supply and warmth and grew more rapidly. Mayhew (1963) had a chuckwalla in captivity that grew from about 82 to 127 mm SV in 13 months. It ate *Tenebrio* larvae during this period, although flowers and lettuce were available.

Sixty-three chuckwallas were recaptured at Lone Butte one to eight times. Their measurements show that growth and aging are dependent on age, sex, social status, and food availability (figs. 1 and 2).

GROWTH AND AGE CLASSES

The marked and recaptured animals were divided into three age classes on the basis of size and maturity. Hatchlings and juveniles were placed in Age Class I, immatures in Age Class II, and the sexually mature in Age Class III.

Age Class I.—Individuals 46 to 60 mm SV were considered hatchlings; those 60 to 99 mm SV were arbitrarily designated juveniles. All chuckwallas in Age

Class I were probably in their first year. Hatchlings occasionally appeared in the fall (October and November) and late winter (February and March). By the end of their first spring, they might have doubled in length; many reached 90 to 100 mm SV in June or July.

Age Class II.—Chuckwallas 100 to 149 mm SV were termed immatures and

TABLE 2

AGE CLASSES AND GROWTH RATES OF CHUCKWALLAS AT LONE BUTTE

AGE CLASS	I	II	III				
Females:							
SV Length (mm)	46–100	100–149	150–169				170–205
Number of individuals		15	6				19
Mean growth/yr (mm)	40–50*	10.866	1.75				.21
Range (mm)		0–25	0–3				0–.7
Standard deviation		7.98	1.66				.2968
Males:							
SV Length (mm)	46–100	100–149	150–169	170–179	180–189	190–220	170–220
Number of individuals		21	14	4	7	18	31
Mean growth/yr (mm)	40–50*	22.95	11.42	9	5.4	.2	4.41
Range (mm)		10–38.3	0–25.9	0–13	0–12	0–8	0–13.5
Standard deviation		7.624	8.24				5.02

* Estimate.

were placed in Age Class II (table 2). Males in this group grew an average of 23 mm/yr (range 10–38) in snout-vent length. These animals were usually in their second to fifth spring. A male might pass through Age Class II in 1.5 years but this was uncommon.

Females grew more slowly; increase in snout-vent length averaged 10.8 mm/yr (range 0–25 mm). The difference between male and female growth rates was significant ($P < .001$). Females remain from three to six years in Age Class II.

Age Class III.—Lizards in this category were potential breeders (see pp. 10–14). Females ranged in length from 150 to 205 mm SV and males from 150 to 220 mm SV.

Males again had much higher growth rates which were significantly different from those of females ($P < .005$). Those 150 to 169 mm SV increased an average of 11.4 mm/yr (range 0–26 mm), whereas males >170 mm SV had a mean growth of 4.4 mm/yr (range 0–13.5).

After reaching 150 mm SV, a female's growth was drastically curtailed. Females 150 to 169 mm SV grew an average of 1.75 mm/yr (range 0–3); those from 170 to 205 mm SV had a mean growth increase of .21 mm (range 0–.7).

I estimate that a 200 mm SV male may have lived a minimum of six springs but is much more likely to be ten or more years old. A chuckwalla is 46 to 60 mm SV when hatched and may double in SV length by the end of its first spring. It could reach Age Class II (100 mm SV) in one year. If its maximum growth during the second and third years is 38 mm/yr (the greatest found in this study), the lizard could attain 176 mm SV and sexual maturity by its third year. The maximum growth recorded for males 170–189 mm SV was 13 mm/yr and for those 190–220 mm SV 8 mm/yr. So a male >170 mm SV in his third

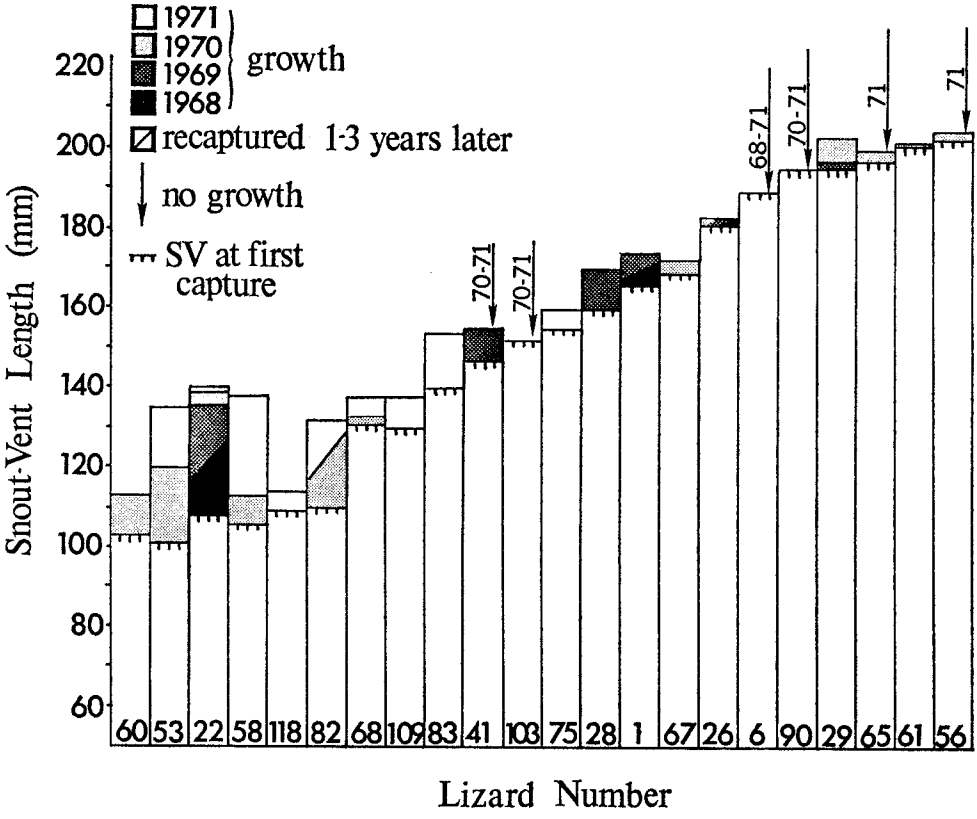

Fig. 1. Growth rates for female chuckwallas at Lone Butte.

year could reach 200 mm SV at the end of his sixth spring. This is a minimal estimate. Using average growth rates from table 2 for each Age Class, a male at Lone Butte would require at least ten years to reach 200 mm SV.

Females would require almost double the time to reach 200 mm SV, even if they grew at maximal rates. If a female attained 100 mm SV at the end of her first spring, she would then take a minimum of two more years to reach 150 mm SV at a growth rate of 25 mm/yr, and six more years or a total of nine springs to reach 169 mm SV. The maximum growth for females between 170–200 mm SV was .7 mm/yr. On this basis it would require forty years to reach 200 mm SV. I think this figure is excessive and I would estimate a total of twenty years: nine years to reach 169 mm SV plus eleven or so to reach 200 mm SV.

Social status.—Social status among males appeared to be an important factor in growth rates. Dominant and aggressive lizards grew more rapidly than subordinates. There were few dominants and many subordinates in the Lone Butte population.

Among the males in Age Class II, the growth of a single dominant was compared with the mean growth of 15 subordinates in an analysis of variance (Sokal and Rohlf, 1969:223–226). The dominant grew 38 mm/yr whereas the subordinates grew an average of 20.6 mm/yr (S.D. 5.87). The growth rates of dominant

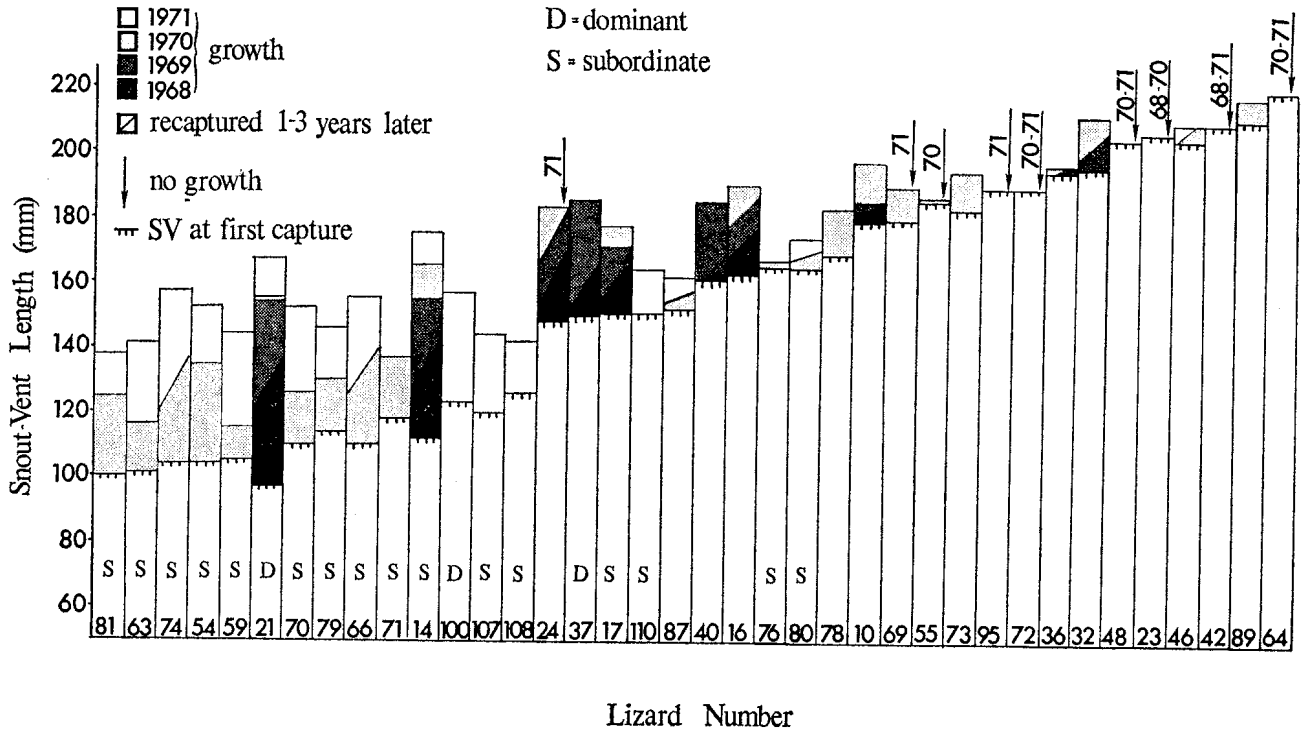

Fig. 2. Growth rates for male chuckwallas at Lone Butte.

and subordinates were significantly different at the 1% level. In Age Class III a single dominant was compared with 9 subordinates. The dominant grew 23.9 mm/yr, whereas the subordinates averaged 6.67 mm (S.D. 4.87). The difference was significant at the 1% level.

Food availability.—Growth occurred primarily from late February, when the lizards first emerged from hibernation, through June. Few chuckwallas grew at all in the summer or over the winter. The growth period is closely associated with availability of food. Wildflowers generally appear in late February, peak in April, and dry up in late May. This varies, however, as flowers sometimes dry up in late April or last until June. Perennials bloom later and last a month longer.

Growth varied according to winter rainfall. In winter of 1969–1970 precipitation was below average and flew flowers bloomed the following spring. In general, average growth for 1970 in males of all age classes was below that for 1968, 1969, and 1971. Males in Age Class II grew an average of 25.13 mm/yr (S.D. 6.7) in the springs of 1968, 1969, and 1971, whereas in 1970 the mean was 15.25 mm/yr (S.D. 10.32). The difference was significant at the 1% level. Males in Age Class III (those 150–170 mm SV only) had an average growth of 16.29 mm/yr (S.D. 9.1) in 1968, 1969, and 1971, compared with 6.29 mm/yr (S.D. 6.9) in 1970. The difference was significant at the 5% level.

Data for growth rates of females were insufficient to test for significant differences.

Age Structure

In order to assess population composition, lizards captured in a given year were grouped according to size and maturity in Age Classes. The age structure of the population (table 3) reflected a low turnover and recruitment rate. Adults formed the bulk of the population: 73.9% in 1968, 65.1% in 1969, 60.2% in 1970 and 63.9% in 1971. Recruitment of juveniles was sporadic and in some years no new individuals were added. Juveniles present in a given year were probably hatched the previous fall. They represented from 0 to 6.9% of the population.

TABLE 3

Population Composition and Sex Ratios

	1968		1969*		1970		1971	
	No. lizards	%	No. lizards	%	No. lizards	%	No. lizards	%
Adult Males	19	73.9	19	65.1	28	60.2	31	63.9
Adult Females	12		9		16		15	
Immature Males	5	23.8	5	30.3	14	32.9	15	36.1
Immature Females	5		8		10		11	
Juveniles	1	2.3	2	4.6	5	6.9	0	0
Total	42		43		73		72	
Sex Ratio	1.47:1		1.26:1		1.81:1		1.88:1	
Sex Ratio of Adults	1.58:1		2.12:1		1.75:1		2.07:1	

* Summer only.

Population Turnover

Mark and recapture data give an inadequate estimate of the animals actually present and of population turnover. Chuckwallas, especially males, have large home ranges and may travel extensively (see pp. 14–16). An individual might spend the spring in one portion of its range and summer at another. In addition chuckwallas can be hard to capture and rapidly become trap shy. Recaptures became increasingly difficult as the study progressed. For instance 2 individuals captured in 1968 were not recaptured until 1971; 3 of the 1968 animals recaptured in 1970 were observed in 1971 but could not be trapped. So the actual number of marked animals present in a particular year was much higher than the recapture range of 35.7 to 76.0% shows (table 1).

Population turnover can be estimated from recruitment and recapture data. Recruitment ranged from 0 to 6.9%, whereas the highest recapture figure was 76% (lowest loss 24%). Population turnover probably falls within the average recruitment rate and the minimum estimates for loss and may be 5 to 25%.

Sex Ratios

Sex ratios showed a strong male bias during the 4 year study (table 3). In 1968 the ratio of males to females was 1.47:1 for the entire population. The 1969 figure of 1.26:1 represents summer captures only. The trend toward male predominance increased in 1970 and 1971 to 1.81 and 1.88:1 respectively. The sex ratio of the 116 animals captured and marked from 1968–1971 was 1.61:1.

At first I thought that males might be easier to capture and were somehow biasing the sex ratios. However by 1971 most chuckwallas encountered were marked. Only 14 new individuals were captured in 1971 and the sex ratio of these was 2.25:1.

Nagy (personal communication), in a study of water balance on the chuckwalla in 1969–1970, also noted an imbalance of sex ratio in favor of males. His study site was 50 miles south of Lone Butte in the Mojave Desert. However Johnson (1965) found a sex ratio of 1:1.09 in favor of females in a population 30 miles southwest of Lone Butte. The 69 animals were captured from 1958–1960.

The situation at Lone Butte appeared unusual; reasons for the imbalance were unknown. Only sex ratios of immatures and adults could be measured, because hatchlings and juveniles cannot be sexed with accuracy until > 100 mm SV. The sex ratio of adults steadily changed from 1.58:1 in 1968 to 2.07:1 in 1971 in favor of males.

Mark and recapture data indicated a greater loss of adult females than males. Sex ratios of immatures (Age Class II) also showed this trend—1:1 in 1968 to 1.36:1 in 1971. Female loss could be due to emigration or mortality. The former is not likely, because female chuckwallas have small home ranges (compared with males) and travel infrequently. The study area was bounded on two sides by unfavorable habitat and was sufficiently large to encompass females who had moved distances of 1 to 3 home range widths away from capture sites.

Reproduction

In order to determine the reproductive cycle of *Sauromalus obesus,* 236 preserved specimens (135 males and 101 females) were examined. These lizards had been collected from February through October from 1908 to 1970 throughout the geographic range.

TABLE 4
Numbers of Female Chuckwallas Analyzed for Presence of Enlarged Follicles

	Size of Females (SV mm)				
	<129	130–139	140–149	>150	Total
March	2	1	2	3	8
April	6	4	6	15	31
May	4	2	6	22	34
June	2	0	3	7	12
July	4	2	2	4	12
August	0	1	0	1	2
September	0	0	0	0	0
October	2	0	0	0	2

Female breeding cycle.—Females examined ranged in size from 50 to 191 mm SV. Most were collected in April and May (table 4).

Females under 140 mm SV did not have enlarged follicles. Most of the small lizards (<120 mm SV) had spherical follicles 0.5 to 2 mm in diameter. Females 120 to 140 mm SV had 2–5 mm follicles. One 134 mm SV female had 6 ovarian eggs 8.5 to 9.0 mm in diameter on May 28.

Females 140 mm SV or larger may have enlarged ovarian eggs greater than 10 mm in diameter in April, May and June. No preserved females collected in March or during summer and fall months had enlarged follicles. This corresponds with field data obtained at Lone Butte. No females were found with enlarged ova during late winter, summer or fall.

The smallest female with enlarged (> 10 mm) ovarian eggs was 145 mm SV. She was collected on June 1, 1941 in Kern Co., Calif., and had 8 ovarian eggs ranging from 15.5 to 18.6 mm. One 148 mm SV female from Sonora, Mexico, had 6 ovarian eggs (11–14 mm) on May 12. Size at reproductive maturity may vary within the geographic range. However, since only 2 females less than 150 mm SV possessed enlarged eggs, I considered animals 150 mm SV or longer to be adults (table 5). All adult females belong to Age Class III.

Twenty of 47 adults collected in spring had enlarged ovarian eggs (table 5). Two had oviducal eggs. Fifteen had eggs 14 to 19 mm in diameter; 5 had eggs 10 to 13.9 mm. These females were captured between May 7 and June 5. Johnson (1965) reported "enlarged follicles" in 5 of 19 females captured between April 19 and May 23. The females ranged in size from 149 to 184 mm SV.

Two females (178 and 169 mm SV) captured at Lone Butte on April 3 and May 3, 1968 were gravid. The latter was waddling across a rocky slope eating pincushion flowers (*Chaenactis Fremontii*) prior to capture. Her abdomen was distended and dragged on the ground.

TABLE 5
SIZE OF OVARIAN EGGS AS A FUNCTION OF SNOUT-VENT LENGTH

	Size of Females (SV mm)			
Egg Size (mm)	129	130–139	140–149	>150
<5.0	20	9	12	25
5.0–9.9	1	1	5	7
10.0–13.9	0	0	0	5
>14.0	0	0	2	15

Not all adult females lay eggs every year. Only 42% of 47 preserved adults collected during the breeding season had enlarged follicles. Johnson (1965) noted that 13 of 19 females collected from May 9 to September 13 were reproductively inactive; he did not mention how many were adults or how many were captured in May and June. Most adult females at Lone Butte did not have enlarged eggs in the springs of 1970 and 1971. In 1971 only 2 of 6 adults captured from April through June were suspected of having eggs (estimated at 5–8 mm in diameter).

Preserved females with large eggs (10–19 mm) had little food in the gut. In many the stomach appeared to be shrunken. Eggs apparently take up much abdominal space usually occupied by the bulky stomach and intestines. Females with large eggs had extensive fat bodies. Hahn and Tinkle (1965) reported that fat stored by females of *Uta stansburiana* at the end of one reproductive season was used for egg production in the next.

Clutch size.—Potential clutch size for 22 females varied from 6 to 13 with a mean of 7.8. All females measured had eggs > 10 mm in diameter. All clutches had 6 or more eggs.

In general larger females produced larger clutches. See figure 3 for a linear regression of clutch size on snout-vent length. Tinkle, Wilbur and Tilley (1970) reported a significant correlation between clutch size and snout-vent length; the two were directly proportional.

Egg laying.—Eggs are probably laid in late spring and early summer. Johnson (1965) captured a female with 7 oviducal eggs on June 17 and observed egg deposition on June 22. Bogert (1930) found oviducal eggs in females collected May 11 and 12. Ted Case (personal communication) collected 2 adult females June 11 and 18, 1970, with 8 and 7 oviducal eggs respectively; another female had 13 on May 30.

There is one report of egg laying and another of oviducal eggs in August, but these were captive animals at the San Diego Zoo (Shaw, 1952).

One female (180 mm SV) who had mated on June 13, 1971, laid eggs in the outdoor pen between July 4 and 7. Egg laying was not observed. On November 22 a single hatchling (57 mm SV, 52 mm VT) appeared. Although the pen was thoroughly searched, the nest site was not found. Time from laying to hatching was 168 to 171 days.

Hatchlings.—Very few hatchling chuckwallas have been found. A single hatchling trapped at Lone Butte on October 22, 1971, measured 47 mm SV. Juveniles were captured in the spring of 1970, but none was as small. A 62

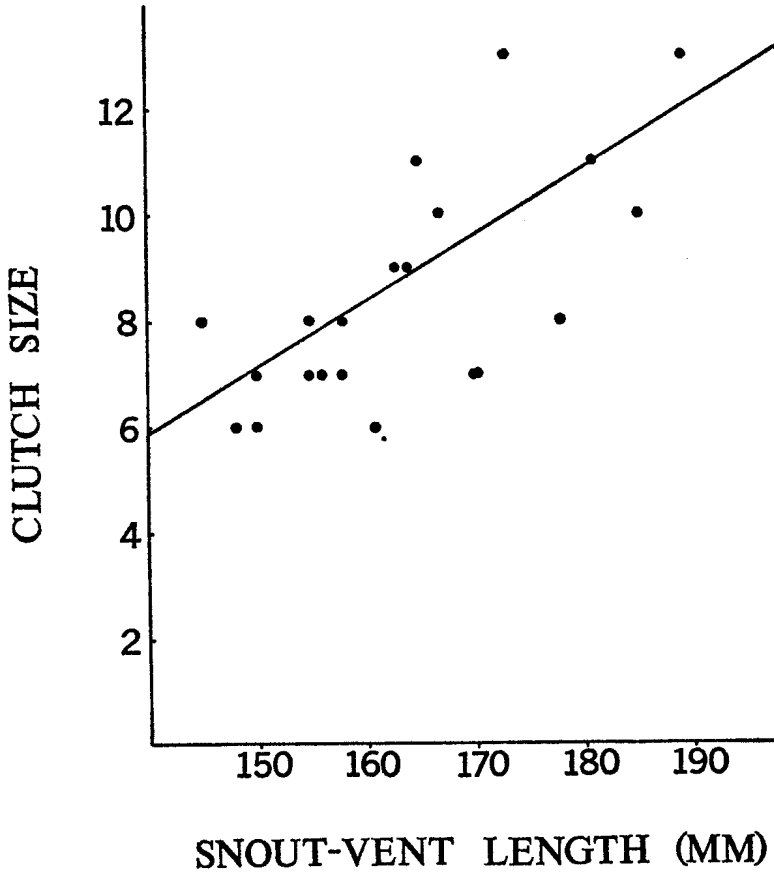

Fig. 3. Clutch size versus snout-vent length in chuckwallas.

mm hatchling was captured on April 4, and 5 juveniles trapped between April 20 and June 7 ranged from 78.5 to 83 mm SV. They probably came from eggs hatched the previous fall.

Eleven small chuckwallas (46 to 78 mm SV) were found in museum collections (out of 550 animals). One 56 mm individual was captured in October and another (63 mm) in September. The rest were found in late winter and spring from February 12 to June 7 (table 6).

Hatching appears to occur in late summer or fall, a time of year when the desert is dry. Temperatures can also be unfavorable; they vary from hot in August and September to cold in November and December. Hatchlings probably go directly into hibernation in the Great Basin region and in the Mojave desert because food is virtually unavailable.

Anomalies.—One 109 mm SV "female" (undeveloped femoral pores) had a large right ovary with 8 follicles 3–5.5 mm in diameter; on the left side was a small testis with *vas deferens*. Another female (185 mm SV) with 10 enlarged ovarian eggs (11–14 mm) had a 20 mm egg capsule lodged in the right oviduct. There was a needle-like stick about 30 mm long that had penetrated the ab-

dominal wall a few mm below the umbilical scar and had entered the oviduct and an oviducal egg. Scar tissue covered the mass and blocked the oviduct

Male Breeding Cycle.—Testes volumes were used as a measure of the approximate time males were able to reproduce. Testes were measured with calipers to the nearest tenth of a mm. Volumes were calculated by using the formula $V = \frac{4}{3} a^2 b$ for an ellipsoid, where a is one-half the width and b is one-half the length of the testis. See table 7 for numbers of males analyzed.

Testis size varied considerably according to season and with snout-vent length. Starting in late March or in April the testes greatly increased in volume

TABLE 6

MUSEUM RECORDS OF HATCHLING CHUCKWALLAS

Museum No.	Date	Snout-Vent (mm)	Vent-Tail (mm)
MVZ 60724	10–?–41	56	55
LACM 61936	4–9–63	63	47
LACM 52892	3–20–67	62.5	65
LACM 52891	3–22–67	46	50
LACM 19308	2–12–61	57	53
LACM 19302	6–7–61	59	53
LACM 19303	6–7–61	61	52
LACM 19330	3–16–47	78	71
LACM 19309	2–12–61	60	58
LACM 19307	2–12–61	74	64
LACM 19326	4–21–51	70	68

TABLE 7

NUMBERS OF MALE CHUCKWALLAS ANALYZED FOR TESTES VOLUME

	Size of Males (mm SV)				
	<129	130–139	140–149	>150	Totals
February				1	1
March	6			7	13
April	4	5	3	28	40
May	3	3	8	26	40
June	5	1	1	15	22
July	4	2		7	13
August	2			1	3
September				1	1
October	1		1		2

until late May or early June. Greatly convoluted seminiferous tubules could be seen through the tunica albuginea. The *vas deferens* also enlarged and became convoluted. After the breeding season, from late June through summer and fall, testes were small and opaque, like an empty sack. Seminiferous tubules were not visible (fig. 4).

The testis volume at sexual maturity was estimated at a minimum of 300 mm^3. At this volume the enlarged seminiferous tubules were usually evident and testis appeared fat and rounded. The smallest males with enlarged testes were 140 mm SV. Two were 140 mm SV and two 145 mm. These four were collected in Sonora, Mexico, on May 11 and 13. No males collected in any other part of the geographic range had testes enlargement below 150 mm SV. The snout-vent length at sexual

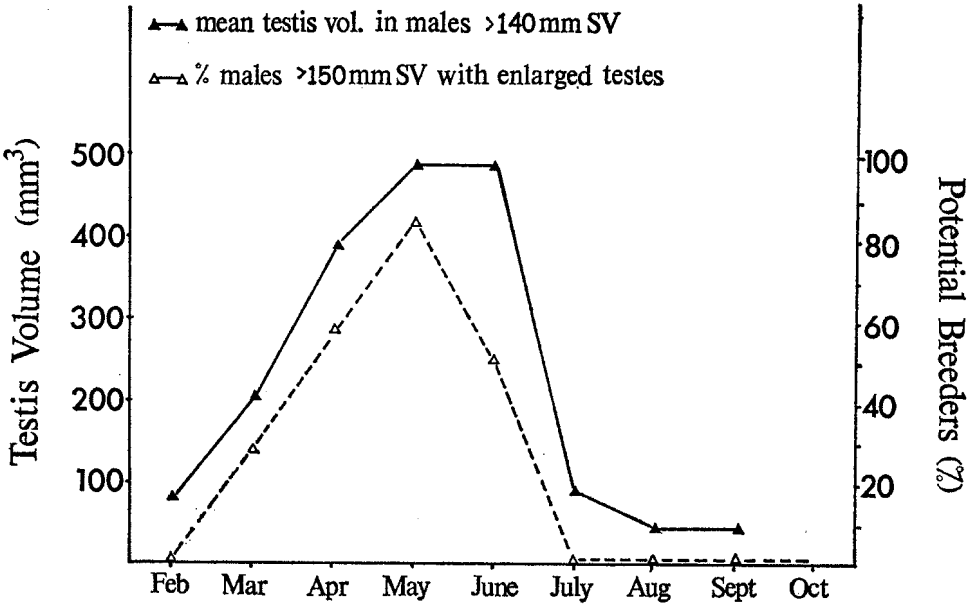

Fig. 4. Testes volume changes in preserved chuckwallas collected throughout the geographic range from February through October.

maturity probably varies throughout the geographic range and may depend on food supply. For the purposes of this study, a male was considered sexually mature and adult at 150 mm SV (Age Class III).

Peak testes volumes occurred in April, May and June (fig. 4 and table 7). There was a rapid drop in volume after mid June. Johnson (1965) found 9 chuckwallas with "enlarged" testes from April 19 to June 7; these varied in length from 152 to 182 mm SV. He also noted that the maximum size of lumen in the seminiferous tubules occurred in May and "the greatest number of sperm tails were observed in gonads collected in May."

Not all adult males (> 150 mm SV) come into reproductive condition during the breeding season. In April, May and June the frequency of adults with enlarged testis was 57, 83, and 50%, respectively. During May, when testis volume peaked, 83% of the males were in breeding condition (fig. 4). Johnson (1965) also reported that not all adults had enlarged testes in spring but did not cite the sizes and numbers.

Population Distribution

Home Range.—I define home range for a chuckwalla as the area frequented per season. The home range is essentially an activity area. During spring, a chuckwalla is likely to traverse its entire home range within a day. In summer it may remain for weeks within a single rockpile and travel only occasionally. Home ranges are not as large as the area with which the lizard is familiar. I had the impression that many lizards knew and had frequented surrounding areas at other times but had chosen a particular range for the season. Some lizards shifted home ranges from year to year.

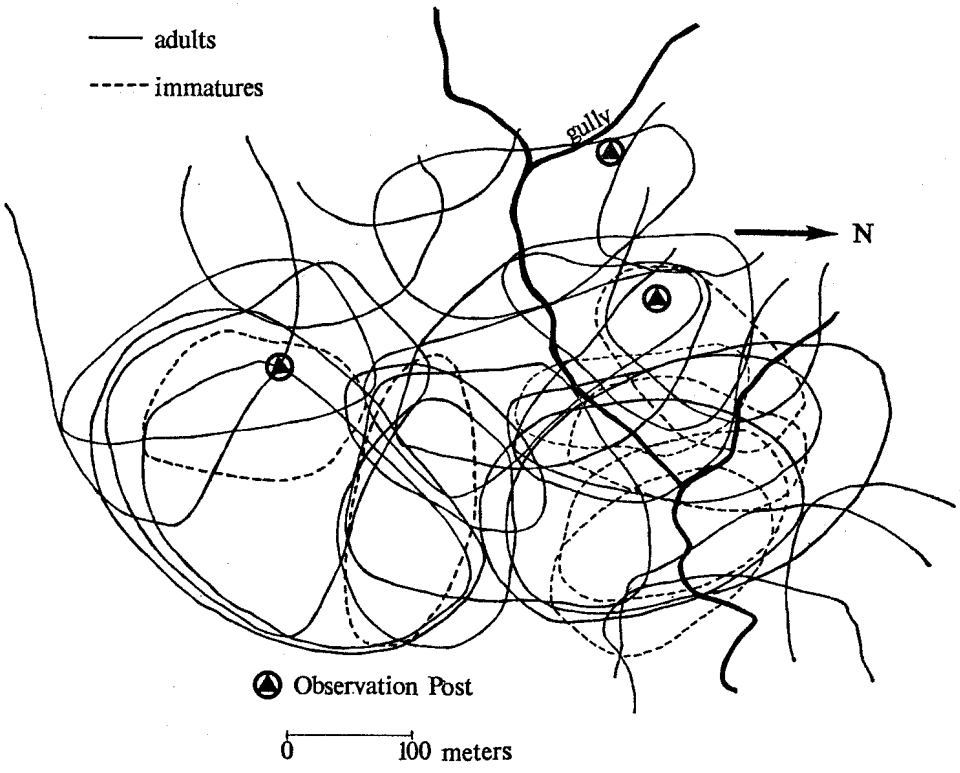

Fig. 5. Home ranges of some male chuckwallas at Lone Butte.

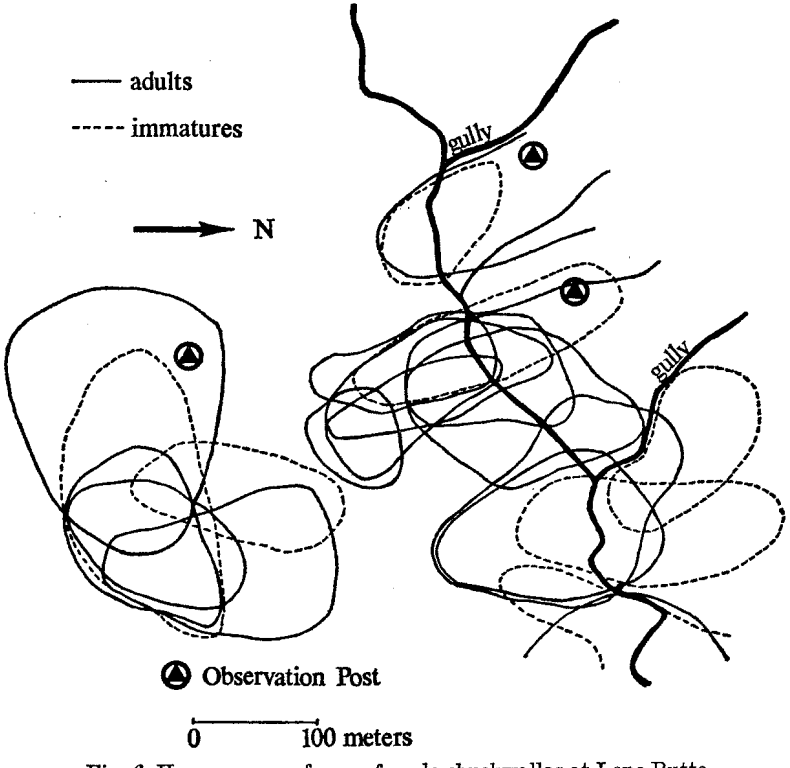

Fig. 6. Home ranges of some female chuckwallas at Lone Butte.

Home ranges were estimated for a portion of the population: 22 adult males, 14 adult females, 11 immature males and 7 immature females. These animals were observed a minimum of 5 days; most were seen several times per month during the spring. Home ranges for males averaged 1.9 ha (range 1–3.3); females 0.81 ha (range .4–1.6); immature males 0.98 ha (range .85–1.5); and immature females 0.72 (range .61–1.1). See figures 5 and 6.

Johnson (1965) found smaller areas for 8 males (0.57 ha) and 5 females (0.17 ha). Schallenberger (1970) reported 1.07 ha for males and 0.67 for females, but did not mention the numbers of individuals used in the estimation. Nagy (1973) reported 0.20 ha for 7 males and 0.17 ha for females.

Home ranges of adult males overlapped extensively and were significantly larger than those of females ($P<.001$). The larger areas reflected the increased movement, aggressiveness and higher activity levels of males. Females also had overlapping ranges but as there were fewer females seen per ha, apparently not as many occupied a given area.

Distribution.—Chuckwallas were localized in the rockpiles and outcrops which were scattered over hillsides and gullies. Usually two adult males did not occupy the same rockpile at any time of year, but females could be found in close proximity. Adult males and females were seen with immature males in 1970 but not in the spring of 1971. In the latter year dominant males did not tolerate young males in the close vicinity. The degree of male-to-male association appeared to be dependent on aggressive levels and time of year.

Density.—The density of chuckwallas per ha was difficult to assess using the Lincoln Index. Random sampling was impossible because lizards moved extensively, were difficult to capture and recapture, and became trap shy.

One portion of the study area was collected intensively in 1970 and 1971. Most lizards were captured; the exceptions were a few juveniles. There were 13.8 chuckwallas per ha (29 males and 18 females) on this 3.4 ha site. Johnson (1965) found 7.1 chuckwallas per ha.

SEASONAL AND DAILY ACTIVITY PATTERNS

Seasonal Patterns

At Lone Butte, chuckwallas emerge from hibernation in mid to late February and are above surface on warm clear days. During March lizards emerge between 10:00 and 11:00 A.M. at air temperatures of 16 to 20°C. Substratal temperatures range from about 24 to 33°C. Lizards bask for 60 to 120 minutes, then feed, travel and interact with another until about 3:00 P.M., when they again bask. Retreat to crevices for the night occurs when the sun drops behind the hills and shadows creep over the basking sites at 4:00 to 5:00 P.M. (fig. 7). Air and substratal temperatures in late afternoon vary from 19 to 28°C and 18 to 38°C, respectively.

In April the pattern is the same except emergence is earlier, at 9:00 to 10:00 A.M. Chuckwallas again remain out until late in the afternoon but most activity is reduced to basking and occasional feeding (fig. 7). During both March and April, lizards fail to emerge if skies are cloudy and air temperatures fall below 20°C, or if the wind exceeds 20 knots. Chuckwallas also avoid rain and will seek cover with a light sprinkle.

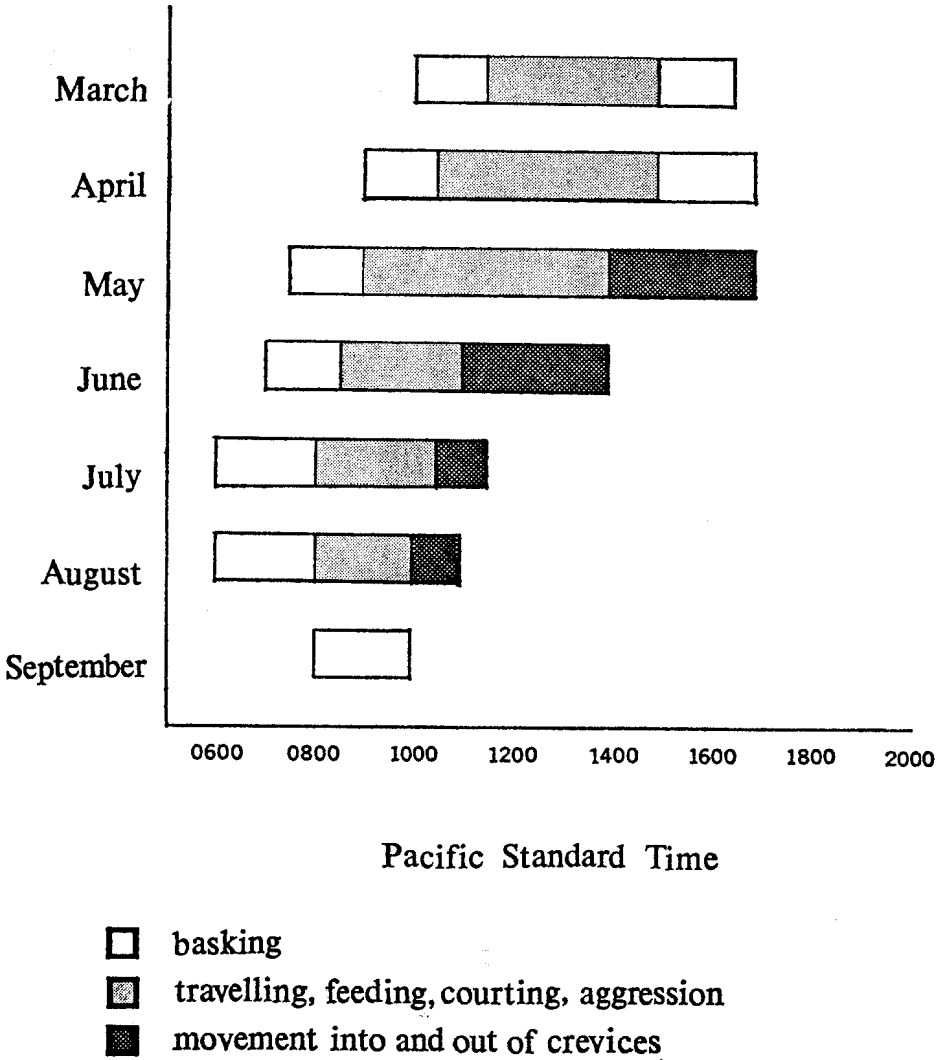

Fig. 7. Seasonal and daily activity patterns of chuckwallas at Lone Butte. This is a summary of data obtained from 1969 through 1971. Courtship was observed only from March through June.

May is warmer and emergence earlier—8:00 to 9:00 A.M. When air and substratal temperatures increase to 32–35° and 38–45°C, respectively, in the afternoons in late May and early June, the lizards retreat into crevices.

By late June summer behavior patterns are well established. Lizards come out at 6:00 to 8:00 A.M. and stay above ground until late morning when air and substratal temperatures exceed 32–37° and 42–50°C, respectively. Lizards bask and feed but travel infrequently and rarely interact. Air and substratal temperatures continue to climb until late afternoon (4:00 to 6:00 P.M.). In general, chuckwallas remain in crevices or underground during afternoon and evening. There are a few exceptions, however; an occasional lizard will come out at dusk. Nagy (1973) reported basking at dusk also.

When days are cool and cloudy in summer, chuckwallas emerge later and remain out longer. In summer they generally do not emerge to bask until air temperatures reach 26–27°C.

Towards the end of August few lizards emerge to bask and on some mornings none can be seen. In September, one or two might appear infrequently. Activity is really over for the season by mid-August. During fall and winter chuckwallas can sometimes be found in crevices, but air and substratal temperatures are usually below 20°C and winds often in excess of 15 knots.

There were more lizards out per day in the spring of 1971 than in 1970, the year of low rainfall (table 8). In 1971, an average of 11.7 chuckwallas were observed per day in March (3.0/observation hour), 15.3 in April (4.45/obs. hr), 24.3 in May (6.0/obs. hr) and 16.5 in June (5.25/obs. hr); whereas in 1970, averages for spring ranged from 7.0 to 14.2 lizards per day (1.64–2.52/obs. hr).

In the summers of 1968, 1970, and 1971, numbers of lizards sighted per day were generally less than the spring figures. They ranged from an average of 5.9 to 6.75 chuckwallas per day in July (1.72–3.4/obs. hr) and 2.3 to 7.5 in August (1.41–1.92/obs. hr) (table 8).

The frequency of males and females observed per day paralleled the apparent imbalanced sex ratio. In the springs of 1970–1971, from 24 to 35% of all lizards sighted were female. In summer, when fewer lizards emerged per day, the frequency of females ranged from 29 to 50%.

TABLE 8

NUMBER OF CHUCKWALLAS OBSERVED (1969–1971)

Month	1969	Obs./hr.	1970	Obs./hr.	1971	Obs./hr.
Mar. av./day					11.7	3.0
range					1–18	
males (%)					69%	
females (%)					31%	
Apr. av./day			7.0	1.64	15.3	4.45
range			1–19		3–28	
males (%)			76%		68%	
females (%)			24%		32%	
May av./day			14.2	2.52	24.3	6.00
range			10–18		15–29	
males (%)			67.7%		65.7%	
females (%)			32.3%		34.3%	
June av./day			7.38	1.76	16.5	5.25
range			1–15		5–22	
males (%)			65.6%		65%	
females (%)			34.4%		35%	
July av./day	6.75		6.08	1.58	5.9	3.40
range	1–13		1–13		4–11	
males (%)	*		71%		57.4%	
females (%)	*		29%		42.6%	
August av./day	7.5	1.92	2.3	1.48	3.4	1.41
range	2–12		0–4		2–5	
males (%)	*		58.8%		50%	
females (%)	*		41.2%		50%	

* Accurate data unavailable.

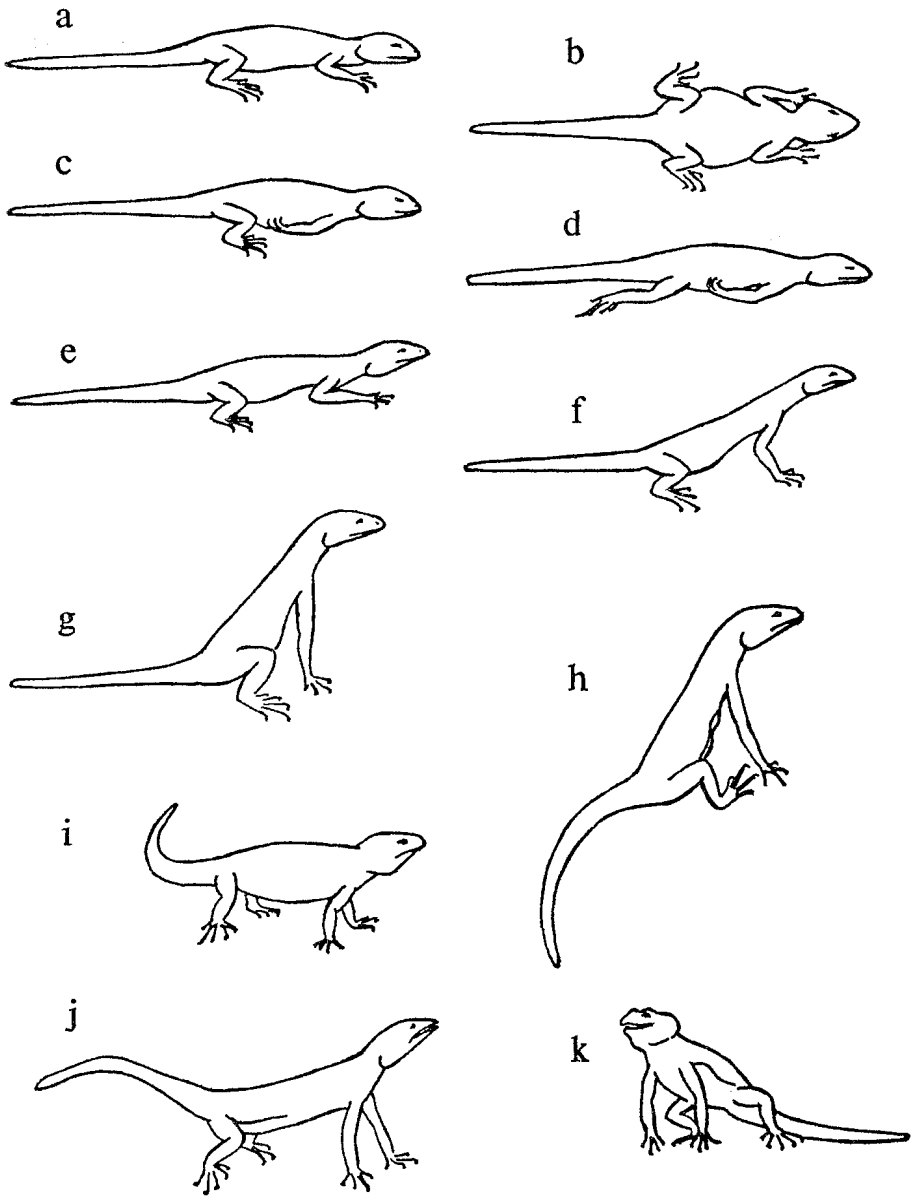

Fig. 8. Basking and resting postures of chuckwallas; *a* and *b* resting or basking; *c* basking with forelimbs extended posteriorly; *d* basking with fore and hindlimbs extended posteriorly; *e* head elevated; *f* head and chest elevated; *g* sitting; *h* stilting; *i* ventral surface elevated; *j* and *k* panting.

Daily Activities

Basking.—Different body postures are used for basking in spring than in summer. In spring, lizards emerge and lie inflated on rocks with ventral surface pressed to the substratum, often resting their throats on the rocks (fig. 8*a–b*). Sometimes the straightened forearms are directed posteriorly and pressed

TABLE 9
FREQUENCY OF FEEDING ON ANNUAL AND PERENNIAL PLANTS

Plants: perennials	1970 spring	1970 summer	1971 spring	1971 summer
Larrea divaricata	28.4%	14.3%	2.29%	20.0%
Ambrosia dumosa	23.0	28.6	3.43	20.0
Dalea Fremontii	4.05	20.0	.57	0
Lycium Andersoni	8.11	0	1.14	0
Bebbia juncea	20.3	0	0	0
Encelia farinosa	4.05	0	.57	8.0
Stephanomeria pauciflora	2.71	5.72	0	16.0
Eriogonum fasiculatum	2.71	0	0	8.0
Eriogonum inflatum	1.35	8.57	0	0
Mirabilis bigelovii	2.71	0	9.70	0
Plants: annuals				
unid. dried annuals	2.71	22.8	.57	28.0
unid. fresh annuals	0	0	28.0	0
Chaenactis steviodes, C. Fremontii, C. carphoclina	0	0	38.40	
Mentzelia affinis, M. albicaulis, M. nitens	0	0	7.43	
Phacelia tanacetifolia	0	0	1.72	0
Phacelia crenulata	0	0	.57	0
Gilia latiflora	0	0	.57	0
Plantago insularis	0	0	.57	0
Eschscholtzia glyptosperma	0	0	.57	0
Rafinesquia neomexicana	0	0	.57	0
Malacothrix glabrata	0	0	1.72	0
Cryptantha sp.	0	0	.57	0
Coreopsis sp.	0	0	.57	0
Erodium sp.	0	0	.57	0

to the sides; some lizards also extend the hind legs in a similar manner (fig. 8 *c–d*). On occasion the head and shoulders are extended from a crevice prior to complete emergence.

Lizards usually face north, northwest or northeast and bask on rocks with a 10° to 60° angle. This posture and orientation expose a maximum of surface area to the sun's rays. As the lizard warms and lightens in color, it first elevates its head, then gradually raises the chest and abdomen from the rock (fig. 8*e–f*). When in the upright, sitting posture the lizard is ready to leave the rock to feed, travel, and interact with other lizards. In spring lizards spend much time basking, not only at the beginning and close of each day, but between feeding, travelling, courting and aggression.

In summer the flattened postures are abandoned. Sitting and stilting are the usual positions (fig. 8*g–h*). Lizards face east, southeast, and northeast into the rising sun. Their bodies are deflated and the lateral folds hang in wrinkles at the sides. Only the pelvic area and tail touch the rock. The dorsal surface is shaded in this posture and heat load is reduced.

Feeding.—Feeding patterns differed from 1970, a dry year, to 1971, a year with average rainfall. In 1970, lizards were observed feeding 99 times, 81 (.46/

obs. hr) in spring and 18 (.224/obs. hr) in summer. Eighty-six percent of foraging occurred in perennial shrubs such as *Larrea, Dalea, Ambrosia* and *Bebbia* (table 9). When feeding in bushes, a chuckwalla usually climbed into the branches from the center of the bush. Its tail spun and hind legs pawed the air as it tried to get its balance and a foothold on the vegetation. In shrubs feeding lasted three to seven minutes. Chuckwallas ate flowers and seeds of *Larrea,* flowers of *Bebbia,* and leaves of *Dalea* and *Ambrosia.* Most annuals eaten in 1970 were dried and were *Schismus* sp., *Plantago,* and *Eriogonum inflatum* (table 9).

In 1971, annuals carpeted the ground and perennials produced fresh shoots and flowers. The most common annual was the pincushion flower, *Chaenactis.* There were at least 15 of these plants per m^2 and all had dozens of white heads in March, April and early May.

Lizards were observed feeding 159 times (.806/obs. hr) in the spring of 1971. From March through June, annuals formed the bulk of the diet (83.3%). The white flowered *Chaenactis* was the favored item. After May 15, when annuals dried up, lizards foraged in perennials in 72% of the observations. They ate leaves of *Encelia,* flowers of *Eriogonum fasciculatum,* leaves and flowers of *Mirabilis,* and flowers and seeds of *Larrea. Bebbia* and *Dalea,* which were favored in 1970, were eaten infrequently.

Nagy (1973) reported that annuals formed about 60% of the diet of chuckwallas in April and May but perennials were eaten thereafter. His study took place in 1970 about fifty miles south of Lone Butte.

Chuckwallas did not eat such shrubs as *Machaeranthera tortifolia, Grayia spinosa* and *Hymenoclea salsola* at any time, although these were readily available. They may have deliverately avoided the lavender flowers of the Mojave aster, *M. tortifolia.*

If winter and spring rainfall is above average, perennials still have green shoots and seeds in summer. If precipitation is below average, shrubs are dry and leafless. In summer chuckwallas do not eat much because there is little or nothing available. Chuckwallas were observed eating 12 times (.161/obs. hr) in the summer of 1969, 12 times (.145/obs. hr) in 1970, and 7 times (.256/obs. hr) in 1971. They ate dried plants—*Ambrosia* and *Stephanomeria,* among others.

HEAD BOB DISPLAYS

Head bob displays of iguanid lizards have been described by Carpenter (1961*a,* 1961*b,* 1962*a,* 1962*b,* 1963, 1966*a,* 1966*b,* 1967), Carpenter and Grubits (1960), Blanc and Carpenter (1969) and others (Fitch, 1956; Hunsaker, 1962; Clarke, 1963; Lynn, 1965; Noble, 1934; and Noble and Bradley, 1933). More recently Ferguson (1971) examined individual and geographic variation of bobbing in populations of *Uta.* Jenssen (1971) studied variation in individuals with age and with geographic location.

Studies to date indicate that head bob displays of iguanids function in intraspecific interactions as well as interspecific associations. Among conspecifics, displays are used in aggression, assertion, courtship, and rejection of males by females. Each species is believed to have its own head bob display. The display is also thought to serve in species recognition.

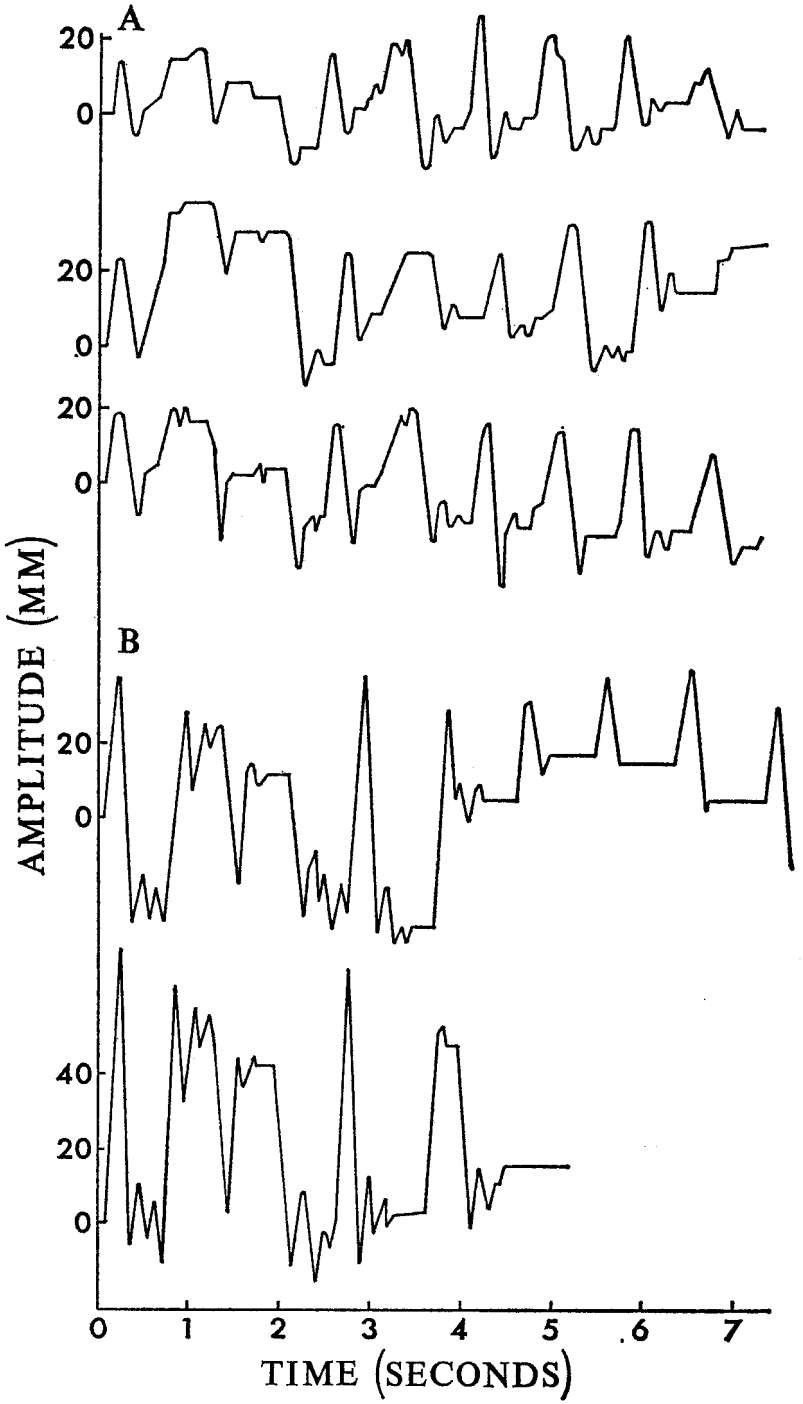

Fig. 9. Head bob display sequences for two male chuckwallas: *a* male 80; and *b* Pen Tyrant.

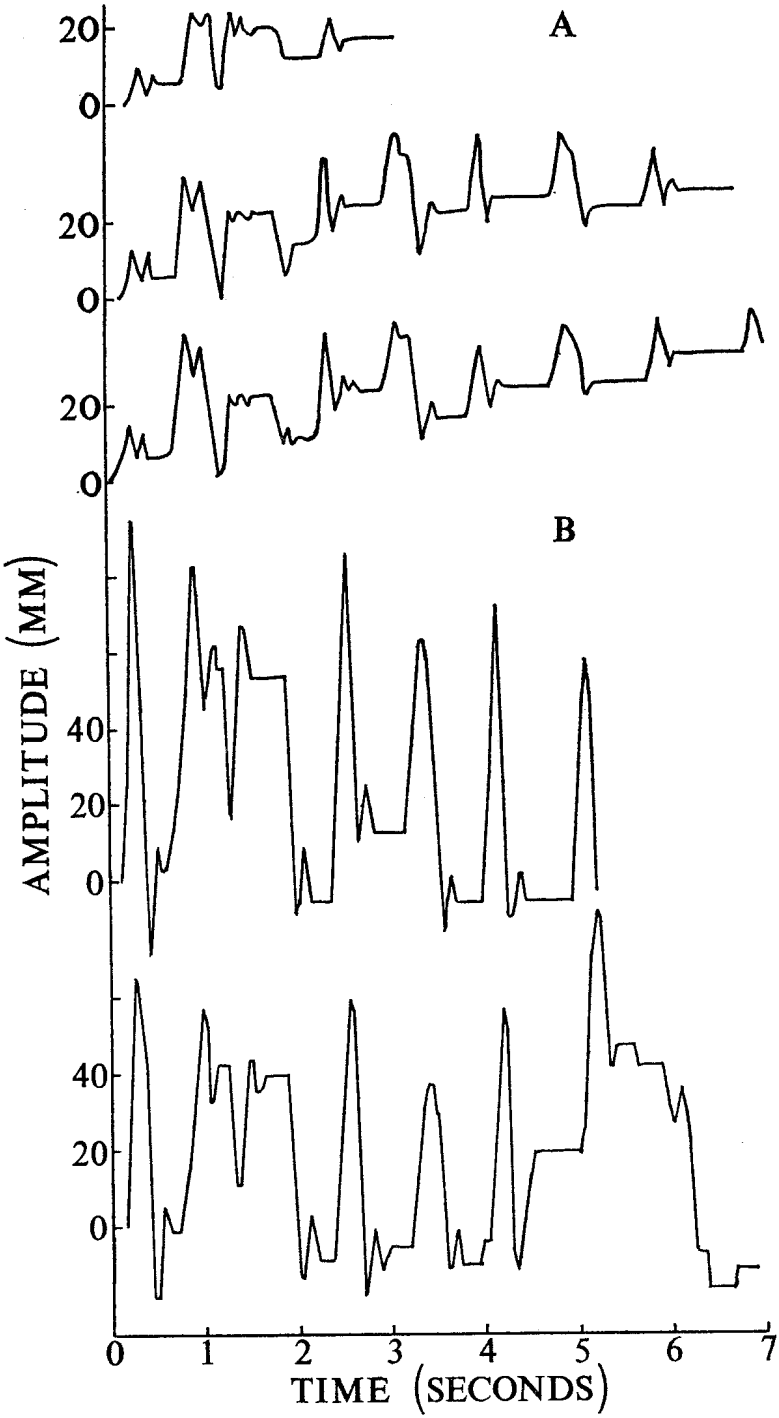

Fig. 10. Head bob display sequences of chuckwallas: *a* female; and *b* male 55.

Materials and Methods

Displays of 13 chuckwallas were filmed in the laboratory and field with 16 mm movie cameras (Kodak cine camera, Canon, and Bolex) at 24 fps. Four individuals, 3 males and a female, were filmed in an outdoor pen and 9 males were filmed in the field under natural conditions. With the exception of the female, all lizards came from one locality.

Several displays for each individual were analyzed frame by frame with a Vanguard Motion Analyzer Model 150C. Only clear side views of the displays were used. Several (five to ten) display action patterns (DAPs) were graphed for each lizard.

The snout-to-eye distance was measured on the lizard and then measured again on the enlarged frames of film in the Motion Analyzer. Using a simple ratio, the actual movement of the lizard during display was calculated in mm. Each DAP graph represents the actual movement of the lizard's head per unit time. There are 24 points for each second of time of the graphs (figs. 9 and 10).

In addition, records were kept of over 2800 displays observed in the field. The type of display, location, posture of the lizard, and general situation were noted.

The Signature

The sequence and cadence of the units of movement for the head bob display are unique for each lizard. There is little variation within the display of an individual but remarkable and visually distinct differences occur between individuals. The first three to four seconds of the display are unique for each chuckwalla; I call this part of the display the "signature." The remaining bobs in the display vary in number and are generally alike for all animals. The number of bobs after the signature depends on display type; assertion displays have few, threat and courtship more, and challenge the most.

Although the first portion of the display is unique to an individual, all chuckwallas use common body movements during displays. Head, neck, and shoulder regions move up and down vertically as the arms flex and extend. The head has a "loose jointed" appearance and can move more extensively than shoulder and chest. Some individuals rock the head back on the neck so that the snout points upward at the peak of the head bob, then snap the snout down so that it touches the substratum when the arms are flexed.

Two or three displays each for 4 individuals are presented in figures 9 and 10. The unique characteristics of the display of male 80 are illustrated in figure 9*a*. Male 80 begins with a single bob, has two slow bobs with pauses at the peak, a fast single bob preceded by a blip (a short, fast bob), and another slow rising bob. Blips occur when the head rocks up and down on the neck. There is no extension and flexion of the forelimbs. The signature of male 80 is contained within the first 4 seconds, whereas the unique portion for the Pen Tyrant (PT) lasts 3 seconds (fig. 9*b*). The Pen Tyrant has a tall peak followed by 2 small peaks or blips, a tall peak with 3 blips at the top, and another tall peak with a pause at the top, followed by a blip.

The female's signature (fig. 10*a*) lasts 3 seconds. Three displays for the female

and two for male 55 (fig. 10*b*) further demonstrate the lack of variation within an individual and the differences between lizards.

The signature phenomenon was first noted in 1970 after films from a few lizards were carefully analyzed. During spring of 1971, there was a marked increase in display activity in the field over that of 1970. Dominant males performed numerous display sequences at one site. It was obvious then that each male had his own pattern. Some had few bobs per second whereas others had groups of two and/or three of different heights. Each peak and dip on the graphs (figs. 9 and 10) were obvious at distances to 100 m with 7 × 50 binoculars.

A lizard may stop at any point in the display. Usually the signature is completed, but in some cases it is not, and the lizard bobs once or twice and stops. In contrast Stamps (1973) described a female anole who continued a head-bobbing sequence to the finish while under attack from another lizard. Although a lizard may stop before the signature is complete, it always starts at the beginning of the display. No lizards were filmed that began displays at the middle or end of the sequence.

Two recent papers (Jenssen, 1971; Ferguson, 1971) discuss variation between and within different populations. Jenssen (1971) found that each *Anolis nebulosus* performed its own displays with remarkable temporal consistency. There were great differences in the lengths of displays but each lizard had the same basic units. However, "without exception the population shared a common pattern." Ferguson (1971) examined populations of *Uta* and discovered more variation between populations than within them.

Analysis of the displays of 12 chuckwallas from one geographic locality revealed a possible population pattern. The pattern has a single fast bob, two bobs of longer duration, and then one or more single fast bobs. The display sequence of an individual appears to be superimposed upon the general population pattern. Timing and the number and sequence of blips are highly individual. Although further research is necessary, these preliminary results provide a strong possibility for individual recognition.

Types of Displays

The signature is used for all displays. Males have four types of displays and females have two. Variable components include amplitude of vertical movement, dewlap extension, and posture. A description of site, position, posture, and parts moved are included in the display types.

Male assertion display.—During assertion, the dewlap is withdrawn, the body is partially or not inflated, and amplitude of head bobbing is low. Lizards usually begin this display with head and chest elevated from the substratum (fig. 8*e–f*). Assertion displays are generally performed after or during travel, after feeding, or after change of position. The display takes place on the ground and on rock-piles, occasionally on a promontory. Other Chuckwallas may or may not be present. I consider this display to be a statement of presence and territory. It is of short duration and has fewer head bobs than the threat, courtship or challenge displays.

Male threat display.—The threat display is always performed in the presence

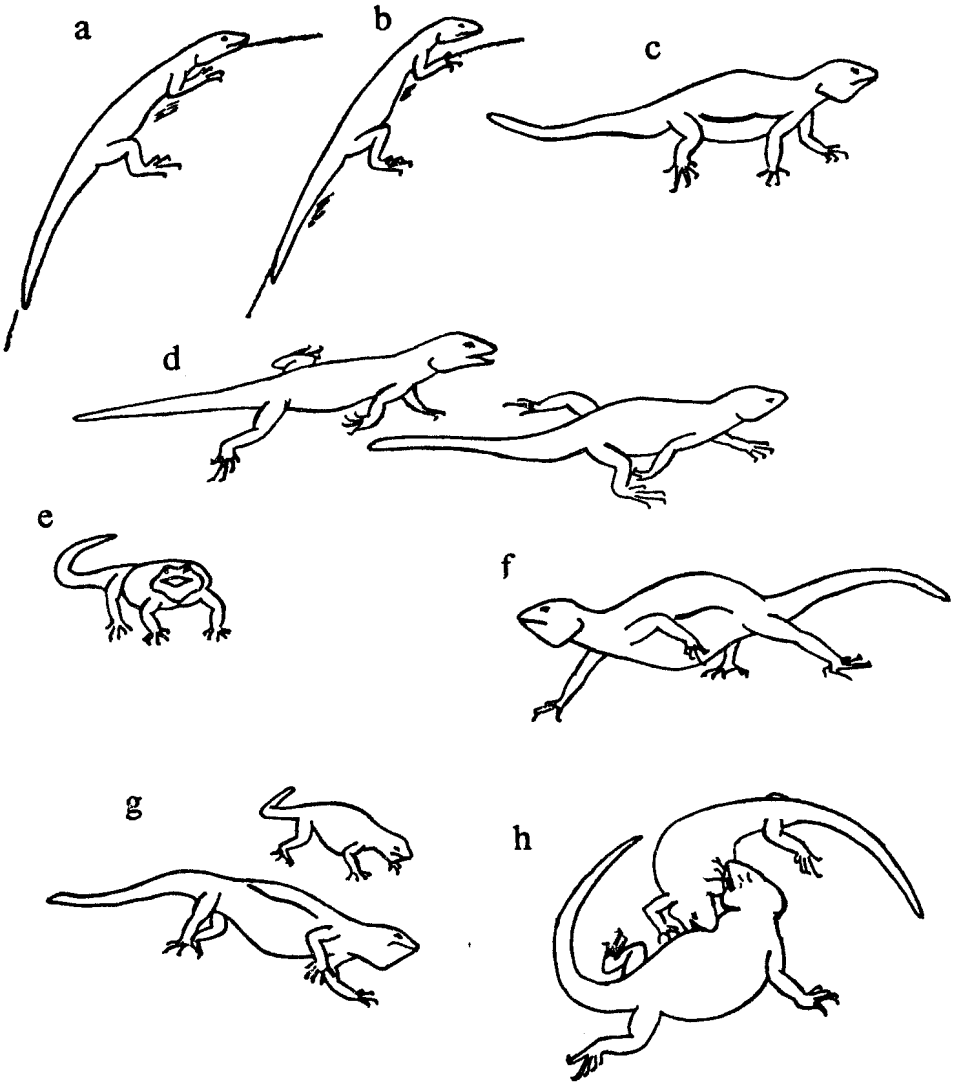

Fig. 11. Aggressive postures in chuckwallas: *a* and *b* "hidden" postures; *c* threat; *d* chasing; *e* open mouth threat; *f* tilting, *g* face-off; and *h* attack.

of another male. It functions as an intimidation or threat, a warning for the other lizard to leave the vicinity or to hide. During the threat, the dewlap is partially to fully extended, the body partially to entirely inflated, and bobbing is of high amplitude. The displaying lizard may or may not position itself parallel or lateral to the intruding animal. The posture of the lizard varies at the initiation of the display (figs. 11*c* and 8*i*).

There are more bobs at the end of the threat display than in the assertion and the threatening lizard usually does several displays, often turning on the rock to take a new position after each display. Frequently the threat will end in a chase.

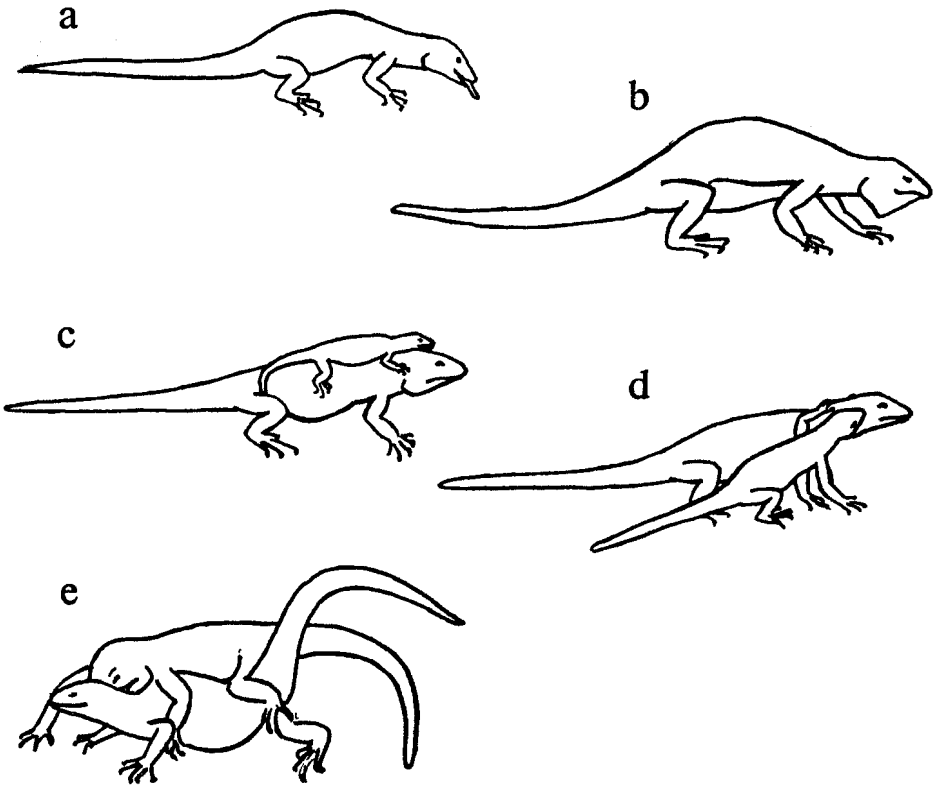

Fig. 12. Courting postures in chuckwallas: *a* licking; *b* male courtship approach; *c* clinging; *d* leaning; and *e* copulation.

Male courtship display.—This display is identical to the male threat display, with the exception of head position and display site. When a male approaches a female to court, he lowers his head to within 2 to 3 cm of the substratum (fig. 12*b*). The display may begin from the lowered head position. If the male has been head bobbing immediately prior to the initiation of a new display sequence, the head and chest are elevated as in the threat or assertion display (figs. 8*e* and 8*i*).

The male does not take any particular position with respect to the female. He may pursue her and pause to display behind her, or he may display beside her, within 5 to 10 cm or more. The female may or may not watch the male display. Courtship displays occur on the ground, in rock crevices, between rocks and on rock tops. Occasionally a pair will court on a rock promontory that has an extensive view of the desert.

Male chuckwallas do not perform the rapid, shallow courtship nodding that is typical of most western hemisphere iguanids. However, two close relatives of *Sauromalus* in the iguanine line have this trait. Both *Ctenosaura pectinata* (Evans, 1951) and *Amblyrhynchus cristatus* (Carpenter, 1966*a*) nod. Avery and Tanner (1971) consider the relationship of *Sauromalus* and *Ctenosaura* to be particularly close; *Sauromalus* is a northern derivative of *Ctenosaura.* A more

distant relative, the monotypic iguanid genus from Madagascar, *Chalarodon madagascariensis,* also lacks this display (Blanc and Carpenter, 1969).

Male challenge display.—The challenge display represents the highest intensity of all the displays. The challenge occurs when 2 males of approximately equal size and aggressive tendencies come into close proximity, or a large subordinate male threatens a dominant by display and by approaching within a few dm or m of the dominant.

The dewlap is fully extended and the body is maximally inflated so that the lateral folds disappear or are only faintly present. The body appears bloated with stiffened, straightened legs protruding from the sides. Both challenging lizards take on this appearance. With heads lowered and backs arched, they display laterally to each other. They usually face opposite directions and are within 3 dm to 1 m of each other. This is called the "face off" (after Carpenter). See figure 11*g*.

The challenge leads to circling. The lizards run rapidly in a circle 2 to 4 dm in diameter, pausing frequently to display. While circling, lizards tilt their dorsal surfaces toward one another, presenting the smooth skin of the back to the opponent. Often the foreleg opposite the opponent is lifted in the air. During circling, one of the lizards often charges the other with open mouth and attempts to bite (fig. 11*e*, Open Mouth Threat). The tilted body presents a smooth, tight surface to the opponent and protects the lateral folds and abdominal skin from exposure to biting. Attacks (fig. 11*h*) may lead to biting on the part of both animals. They roll over several times on the ground, with bodies entangled and tails thrashing wildly. Sometimes fights last several minutes.

One could frequently pick the winner at the start of a challenge display. The winner or dominant was more inflated, had his dewlap more fully extended and did more head bobs. The dominant appeared larger in size, although the snout-vent length of the two opponents was nearly equal and differed only by a few mm.

Males use the same basic sequence and cadence of units for all of the displays. Variations that occur are primarily of intensity, i.e. dewlap extension, amplitude of head bobs, and number of head bobs. The display forms grade into one another and with the exception of the challenge are often difficult to separate.

Use of the tail.—Chuckwallas sometimes violently lash with the tail when capture is attempted or when prodded in a crevice or under a rock. Carpenter (1967) has suggested that *Sauromalus* might use tail slapping during a ritualized fight, usual manner (Type I, see pp. 42–43), and the female at one point arched her tail slapping in any of the fights observed in the field or in the pen. However when the lizards roll over and over on the ground entangled and biting, they thrash and slap their tails.

Female assertion and threat displays.—Very few female displays were observed in the field. Only 1 female (out of 5) displayed in the out-door pen. When travelling or after eating, a female may rarely perform a short assertion display with dewlap withdrawn, body deflated, and with bobbing of low amplitude. On a few occasions, one female threatened and attempted to intimidate another. The dominant female had the dewlap extended, was partially inflated, and performed high amplitude bobs.

Female displays during courtship.—Two large adult females (200 and 205

mm SV) performed another type of display. This was done only during courtship, while a male was displaying or within a few seconds of completion of his display. Often the female would start bobbing with the male at the initiation of his display, and the bobs would be in synchrony for a second or two. She might start and stop repeatedly. Sometimes she would remain motionless during the courtship display and then bob a few times after completion of his display. The female head bobs did not appear to have a pattern.

Unfortunately I was unable to film this. This display was not a typical feature of courtship and did not appear to be aggressive or rejective in nature. It is possible that either the two females possessed masculine traits or that female courtship bobbing is a characteristic of experienced females of advanced size and age and may function in cementing the male-female bond. The latter possibility is suspect because two other females of equal size did not bob during courtship.

Rejection displays.—Many female iguanids have a rejection posture to discourage male advances (Clarke, 1963; Carpenter, 1967; Fitch, 1956). The female usually arches her back in a dome, extends her hind legs, raising the hindquarters off the substratum and lifts or swings her tail from side to side. The posture is often postnuptial and is characteristic of a mated, gravid female.

Female chuckwallas may have such a posture but few were observed with males after mating in June, and after late June no pairs were seen. Once a female arched her tail in the presence of a male. On June 6, tyrant 46 and a female courted together on a rocktop; they had mated the previous day. Courting took place in the usual manner (Type I, see pp. 42–43), and the female at one point arched her tail when the male was posterior to her cloaca. He immediately crawled over her and courtship continued. This was the only observation that resembled iguanid rejection postures, but the tail arch did not appear to serve that function.

A female in the experimental pen did assertion displays when a male approached and stepped on her. She also did assertion head bobs when a male approached within 20 to 30 cm in late summer. This type of activity was not observed in the field.

Role of the Display

During the summer of 1969, 14 displays (.188/obs. hr) were noted in 5 separate situations; during 1970 (April–August) 55 in 21 situations (.195/obs. hr), and during 1971 (March–August) 2791 in 551 situations (12.4/obs. hr).

Display frequency during July and August of 1969, 1970, and 1971 was lower than for spring, reflecting the greatly reduced activity of summer months (see pp. 17–18). Reduced activity is attributed to high daily mean and maximum temperatures and lack of food. Chuckwallas obtain water only through their food. They are subjected to body water stress in summer when annuals are dead and perennials are dry. Nagy (1972) found that reduced activity "resulted in a considerable reduction in metabolic rate, and an even greater drop in water loss."

The great discrepancy in numbers of displays observed during springtime in 1970 and in 1971 was associated with winter rainfall and food availability.

Dominant adult males, who were at the top of the social hierarchy (see pp. 31–34), were involved in most of the display situations and performed the bulk of the displays (table 10). During the summer of 1969, dominant males performed

78.6% of the displays in 80% of the situations. In the spring and summer of 1970, the dominants accounted for 81.7% of the displays in 66.6% of the display situations.

TABLE 10
FREQUENCY OF DISPLAYS AND DISPLAY TYPES IN CHUCKWALLAS

	1969		1970			1971			1969–1971
	summer	total	spring	summer	total	spring	summer	total	total
No. of display situations	5	5	18	3	21	548	3	551	577
No. of displays (obs./hr.)	.188	.188	.269	.099	.214	14.1	.185	12.4	2860
No. of displays (total)	14	14	47	8	55	2786	5	2791	
Assertion	6	6	7	0	7	219	2		
Courtship	0	0	15	0	15	1507	3		
Aggression	8	8	23	8	31	926	0		
Unknown	0	0	2	0	2	134	0		
Lizard performing display									
Dominant male	11	11	43	2	45	2366	1	2367	2423
Subordinate male	0	0	2	4	6	308	4	312	318
Immature male	0	0	0	0	0	54	0	54	54
Female	3	3	2	2	4	58	0	58	65

Subordinate males (see p. 38) were second in frequency of displays. Subordinates were not seen performing displays in the summer of 1969, but performed 6 (10.9%) in 1970 and 312 (11.2%) in 1971. Females and immature or juvenile chuckwallas (<150 mm SV) accounted for a very small number of displays. Females were seen performing 3 displays in 1969, 4 displays (7.3%) in 1970 and 58 (2%) in 1971.

Juveniles were less active in head bobbing than females. A hatchling was observed displaying only once. On May 27, 1970 two hatchlings (in their first spring) were in close proximity. One attempted to climb onto a rock where the other was basking and eating *Encelia*. The basking lizard charged the other and chased it to the base of the rock, returned to the rock top, and did one display.

Displays were placed in five categories, as described earlier: courtship; assertion; intimidation or threat; chasing and fighting; and finally, display situation unclear.

The courtship situation accounted for 54.1% of the displays in 1971. Many more courtship displays occurred than were logged, as courting for a given pair might last for an hour or more, during which time observations were also made on other lizards. In 1970, 27.3% of the displays were of courtship type.

Intimidation, threats, chasing and fighting are aggressive situations and as such were placed under a single heading. In summer of 1969, 57.1% of 14 displays observed were aggressive. In 1970 and 1971, 56.5% of 55 and 33.2% of 2791 displays were aggressive, respectively.

Relatively few displays fit the assertion category. Although 42.9% (6) of the 1969 summer displays were assertive, only 12.7% in 1970 and 7.9% of the 1971 displays were of this type. In general, a chuckwalla does not walk about doing head bob displays unless another lizard is present and the two are interacting in courtship or in an aggressive manner. Another lizard was obviously present in

71.3% of 577 display situations. This behavior contrasts markedly with that of utiform and sceloporine lizards which do frequent solitary displays in spring and summer.

Role of the Display in Interspecific Associations

Chuckwallas use threat displays when with other species of lizards, such as the side blotched lizard (*Uta stansburiana*), collared lizard (*Crotaphytus collaris*), desert spiny lizard (*Sceloporus magister*), and the desert iguana (*Dispsosaurus dorsalis*). Chuckwallas were observed with one of these species on 21 occasions.

Eleven associations were noted with spiny lizards, 6 with collared lizards, 3 with utas, and 1 with a desert iguana. Most of the interactions were aggressive (80.8%). During 8 interactions the chuckwallas did one or more threat displays and either attempted to intimidate or dislodged the other lizard from the rock. Seven of the 8 displaying chuckwallas were male adults; 1 was a juvenile who intimidated a large male spiny lizard with challenge displays. Two chuckwallas chased utas; they may have been attempting to catch and eat them. One male chased a spiny lizard and another a collared lizard.

Once a uta performed several challenge displays with arched back and twitching tail 30 cm from an adult male. The latter did not respond. Once in 1970 and again in 1971 a male collared lizard lay and basked on the back and head of a chuckwalla. The chuckwallas eventually shook them off.

SOCIAL STRUCTURE AND ORGANIZATION OF THE POPULATION

The Tyrant

The social structure and organization of a chuckwalla population are controlled chiefly by the dominant males. These dominants are called tyrants (after Evans, 1951). A chuckwalla tyrant is a large, aggressive adult male with a full length or regenerated tail, who possesses both a harem and a territory, and who controls the behavior of subordinate males.

Tyrant size.—Most large males in the population were tyrants. Twelve males fit this category in 1971. Their average size was 191.3 mm SV (range 183–220 mm SV). Some males that were not tyrants fell within this size range, however. Five of the active subordinates were within the size limits but did not manage to hold territories. Two of these had recently lost their tails.

The large size is an advantage for at least three reasons: experience, dominance, and tolerance of heat load. Size usually reflects age and experience. Although males reach sexual maturity when 150 mm SV, the minimum tyrant size was 183 mm. So the smallest tyrant would have been sexually mature for at least 2 years and would have survived a minimum of 6 springs before attaining tyrant status (see pp. 5–6). During this period the lizard familiarizes himself with his home range and potential territories, takes part in aggressive encounters, and can acquaint himself with his conspecifics.

In most, if not all, of the aggressive situations observed, the individual who emerged as dominant was the largest. If a male is to attain the tyrant status, he usually must be the largest male in a particular area. This explains why certain subordinates who were greater than 183 mm SV did not become tyrants. Two such individuals shared a large portion of their home ranges with a 220 mm tyrant.

Their other borders were surrounded and enclosed by tyrants of snout-vent lengths larger than their own.

Large body size is also an advantage to the tyrant in terms of heat load. In early spring when air and substratal temperatures are cool (18 to 20°C), heat retention is a problem. The tyrants emerge 60 to 120 minutes before subordinates and females and they spend 60 to 90 minutes basking. A large body cools more slowly than it heats (Bartholomew and Lasiewski, 1965) and thus a tyrant can be active for longer periods than the smaller lizards. During May and June, when courtship and mating activities peak, air and substratal temperatures often exceed the maximum tolerances of chuckwallas. Lizards with large body size require more time to warm up and reach critical maximum temperatures than smaller ones do. They therefore can remain above ground and active for longer periods. I also observed tyrants panting in Many and June, ostensibly to reduce body temperatures. Subordinates and immature males only panted after being chased.

The tyrant and his tail.—It appears that a tyrant must have a complete or regenerated tail. If more than a few cm are lost, the male loses his social status. The minimum tail length of a tyrant (regenerated) as expressed in percent of snout-vent length was 65%. For example, male 36 (197 mm SV) was the dominant in a 50 m wide by 5 m high rockpile from 1968 through 1970. Although he was missing the left hand and forearm, 36 was a tyrant and courted the same female for 3 years. During the summer of 1971 his tail was chewed off, presumably by a predator. Tail length was reduced from 150 mm to a 53 mm stump (26.9% of SV length). During 1971, 36 was inactive; he was observed basking and feeding but took no part in courtship, aggression, or head bob display activities. Another tyrant courted his female and pre-empted his rockpile.

Male 55 is another case. During recapture in April 1970, the tail of 55 was inadvertently broken from a length of 168 to 101 mm (54% of SV length). This lizard was inactive for the rest of the season. He was seen slinking from rockpile to rockpile in a submissive manner and is believed to have spent most of the spring and summer in hiding. In 1971, with a large portion of the tail regrown, 55 became the most aggressive of the tyrants.

Male 10 was also reduced from dominant status in 1970 to inactivity in 1971 through tail loss.

The tail appears to be important in balance during walking, running, climbing, and feeding. A sizable tail is useful during mating. A male that loses 30 to 50% of his tail appears to sustain psychological as well as physical damage and thus loses social status.

Territories.—A tyrant possesses, defends, and actively patrols a territory from late February until the end of the mating season in June. Although there were 12 tyrants on the 15 ha study area in 1971, the territorial area was computed for only 8. The defended areas observed for the other 4 included only a portion of their territories and of the study area (figs. 13 and 14).

Territories ranged in size from 3125 m^2 (0.31 ha) to 15,780 m^2 1.58 ha) with an average of 8181 m^2 (0.8 ha). All had several rockpiles or rock ridges with numerous crevice retreats. All appeared to have the same or similar supply of annuals and perennial plants.

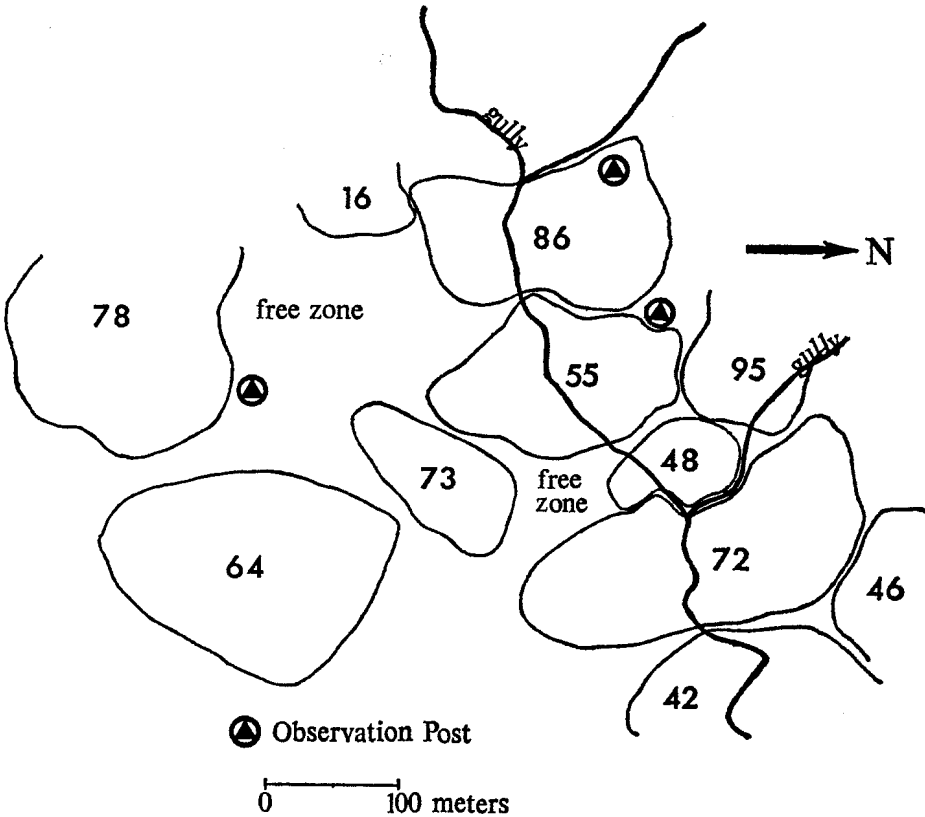

Fig. 13. The territories of tyrant chuckwallas from March through April at Lone Butte.

Territories of tyrants were smaller than their home ranges. However tyrants spent the majority of their time within their territorial boundaries in spring. Territories were superimposed over the numerous home ranges of subordinates and females. Each territory contained portions of home ranges for several other lizards—subordinate adult males, immature males, and females (see figs. 5 and 6 for home ranges of males and females).

Territorial boundaries remained static for most tyrants throughout the late winter and spring. By mid-March the situation was stable, with two exceptions. Figure 13 delineates the areas during March and until April 16. At that time a tyrant, known as the White Back, WB (not captured), moved into the northern territory of male 72, a tyrant with one of the more extensive areas. By the end of April, WB had assumed control of the northern half of the territory of 72. Male 72 and his harem then moved into and remained in the southern half of the territory of 72.

Between April 29 and May 4 a second incident occurred which left a void. Male 48, who was first captured and marked in 1969, disappeared completely. This tyrant had fought with 95 on several occasions over mutual boundaries earlier in the spring. At the time of the disappearance of 48, 95 appeared with a deep gash from shoulder to wrist that penetrated to the bone and a slash in the abdomen

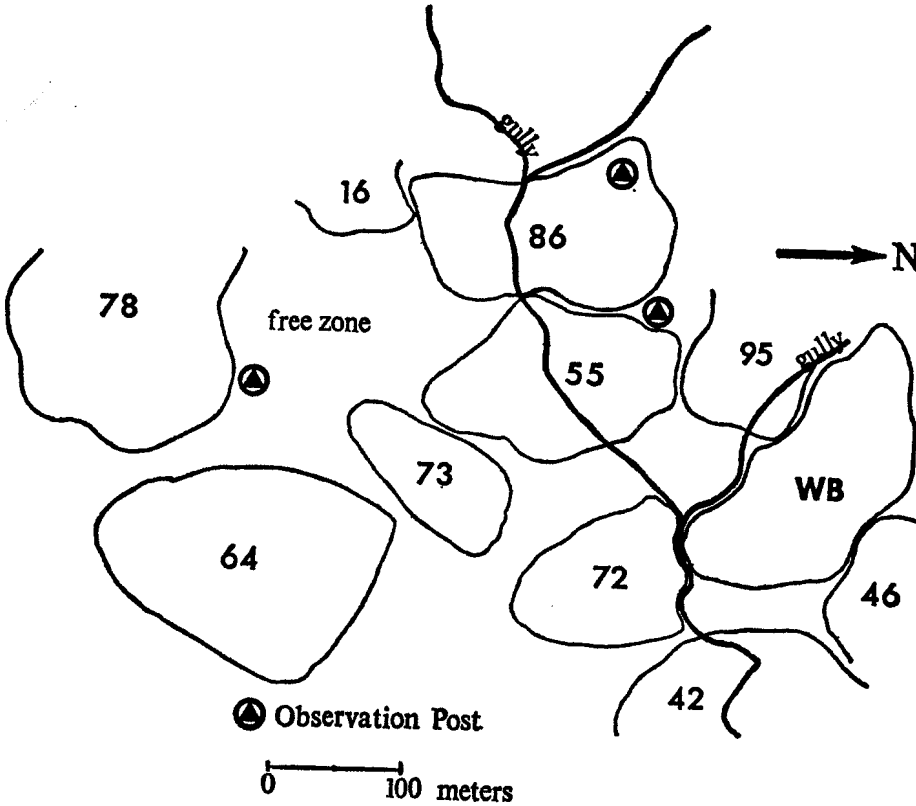

Fig. 14. The territories of tyrant chuckwallas from May through June at Lone Butte.

which exposed the peritoneum. It is possible that 95 and 48 had a final battle, 48 lost, and either was mortally wounded or fled. I feel that the former is more likely as male 48 had lived in this area for at least 2 years and was observed almost daily in 1971 until May 4. The disappearance of 48 could be unrelated to the damage sustained by 95, however.

In any event, boundaries had changed by May 5 (fig. 14). Although male 95 travelled into the former area of 48 several times, he made no attempt to acquire territory. Two subordinate males frequented the area but neither emerged as tyrant nor held the area as a territory. Number 95 became less active during May as his arm swelled and became useless. He was last observed on June 1, barely able to move about. No subordinate or tyrant moved into his territory.

Territorial behavior ceased in mid to late June, at the close of breeding season. This has also been noted for *Amblyrhynchus* (Carpenter, 1966*a*), *Anolis nebulosus* (Jenssen, 1970) and *Crotaphytus collaris* (Fitch, 1956), among others.

Tyrant activity.—Tyrants were the most active of the lizards in every way—movement, daily activity periods, feeding, head bob displays, courting, and aggression. During late winter and early spring, they were the first to emerge in morning and last to retreat in late afternoon. They were above ground most of the day. They frequently occupied prominent positions and displayed vigorously, generally advertising their presence.

Methods of Domination

Tyrants maintained dominance over subordinate males by three techniques: intimidation or threat; chasing; and fighting. In turn, subordinates used these same methods in maintenance of a dominance hierarchy.

Intimidation and threat.—Intimidation or threat, the least aggressive of the techniques, was accomplished by display from a prominent basking site or at a site noticeable to the subordinate. Intimidation was especially effective in ridding the territory of immatures or small adults. The mere presence of a tyrant 20 to

TABLE 11

A Summary of Aggression in Chuckwallas at Lone Butte

	1969	1970		1971	
	Jul–Aug	Apr–Jun	Jul–Aug	Mar–Jun	Jul–Aug
Type of encounter					
Intimidation	1	8	0	54	10
Chase	1	8	4	43	8
Fight or chase-fight	0	0	0	13	0
Lizards involved					
Tyrant to tryrant	2	0	0	11	0
Tyrant to adult male	0	5	0	79	0
Tyrant to immature male	0	1	1	9	0
Adult male subordinates	0	6	1	23	1
Male immatures	0	1	1	3	0
Female to female	0	1	2	2	0
Female to male	0	1	0	0	0
Totals	2	15	5	128	1
Totals per Observation Hour	.0269	.0855	.062	.65	.0367

30 m away might cause a juvenile or immature to back down the far side of a rock and flatten the body in a "hidden" posture (fig. 11*a-b*). Head bobbing was a signal for the subordinate to disappear or leave the territory of the tyrant. During 1970 and 1971, intimidation accounted for 40% of 20 and 50% of 128 aggressive encounters observed, respectively (table 11).

Chasing.—Intimidation and threat were not as effective in dispatching larger males. If numerous threat displays failed to remove a subordinate from view, the dominant would charge at and chase the subordinate. Occasionally the dominant would run at the subordinate without the preliminary warning of the threat display. Chasing was an effective means of dealing with immature and large adult subordinates.

During chase the dominant frequently snapped at the opponent and in some cases leapt onto and rode his back. Once the dominant, while riding the subordinate, turned his head in a snout-down, vertical position and with back arched attempted to bite the pineal region of the opponent. This attack did not resemble copulatory postures. *Amblyrhynchus cristatus* (Carpenter, 1966*a*) is known to chase and "back ride."

Chase accounted for 60% of aggressive maneuvers in 1970 (12) and 39.8% (51) in 1971. The length of chase ranged from 1 m to 75 m with a mean of 19.7 m in 64 cases. The subordinate was pursued until he found cover. Even then a tyrant

might attack him in a crevice or under a rock.

Tyrant 55 frequently chased 80:

On April 29 at 1:00 P.M. 55 was courting a female at the gully edge. At the base of the lookout, 100 m to the north of the courting pair, male 80 was walking about among rocks, licking the substrate. At 1:04 P.M., 55 left the female and ran towards 80. When the tyrant was about 30 m away, 80 started to run east and disappeared from view behind a boulder pile. The tyrant continued to travel toward the site where 80 was last seen and did several threat displays. Between 1:06 and 1:20 p.m. 55 moved about in the vicinity. The tyrant found 80 and at 1:20 chased him to the north and east 50 m. Both then paused. The tyrant did numerous head bob displays from a rock promontory, while 80 rested on the ground at the base of a creosote bush 4 m away. The tyrant continued to display until 1:37 P.M., when he again charged at 80 and chased him in circles twice, then out of view behind a ridge. From 1:41 until 1:47 P.M., 55 did threat displays in the vicinity of the chase, then left to court another female. The tyrant chased 80 a total of 100 m after travelling 70 m to reach him.

Tyrant 64 (220 mm SV) also chased other lizards frequently. On April 4, tyrant 64 observed a fight between two immature males, 71 and 113, 20 m away. These two were circling 14 to 20 cm apart, tilting their inflated bodies toward one another, and occasionally pausing to perform challenge displays from 2:15 P.M. until the smaller of the two, 71, left at 2:30 P.M. At 2:30 P.M., 64 ran down the slope toward the winner, 113, and chased him. They covered a distance of 59 m before 113 disappeared under a rock.

Fighting.—Physical combat was observed only during 1971 and composed 10.2% of the aggressive encounters (see p. 28 for a description of the fighting). Nine of 13 fights involved tyrants; 5 of the 9 were tyrant-to-tyrant encounters which ended in a retreat of both lizards. This was termed "a draw," as there was no winner. These encounters took place at sites where the boundaries of 2 territories met. The other 4 fights with tyrants involved subordinate adult males. Two fights also occurred between immature males and 2 between adult subordinate males.

Fights ranged from 4 to 50 minutes in length, with a mean of 15.7 minutes. Eleven of the 13 combat interactions occurred in March and April (table 11). One each occurred in May and June. This reflects the general trend of aggression in 1971, with a greater number of agonistic occurrences in March and April than in any other month.

The first fight occurred on March 16 at 12:03 P.M.:

The IB male was sighted at 11:58 A.M. on a pink rockpile doing head bobs. He left at 12:00, travelled 15 to 20 m south of the previous lookout, and did more assertion head bobs upon arrival at a new rock. Male 69 was on the ground at the base of this rock, 1 m away. Both lizards faced north. The IB male did no threat display, but 69 did 2 single head bobs; then the former rushed off the rock toward 69. Both lizards were inflated. Facing opposite directions and about 30 cm apart, they circled with bodies tilted inward toward the center of the circle and toward each other. Both presented a flat oval surface to the opponent (figs. 11*f–g*). They circled about five times, running very rapidly, then stopped. Both performed several challenge displays with IB doing more than 69. After circling again twice at high speed, they fought—biting, thrashing, and flipping in the sand. They were snappng at legs, tail and head. IB chased 69 a few meters, then both circled several times. Male 69 broke away from the circle and ran north a meter while IB did challenge displays. Male 69 was not inflated and did not have his dewlap extended. IB male moved parallel to and about 30 cm from 69 while doing more displays. He lunged at 69, who ran north. Male 69 then stopped and did head bobs, with his body at a

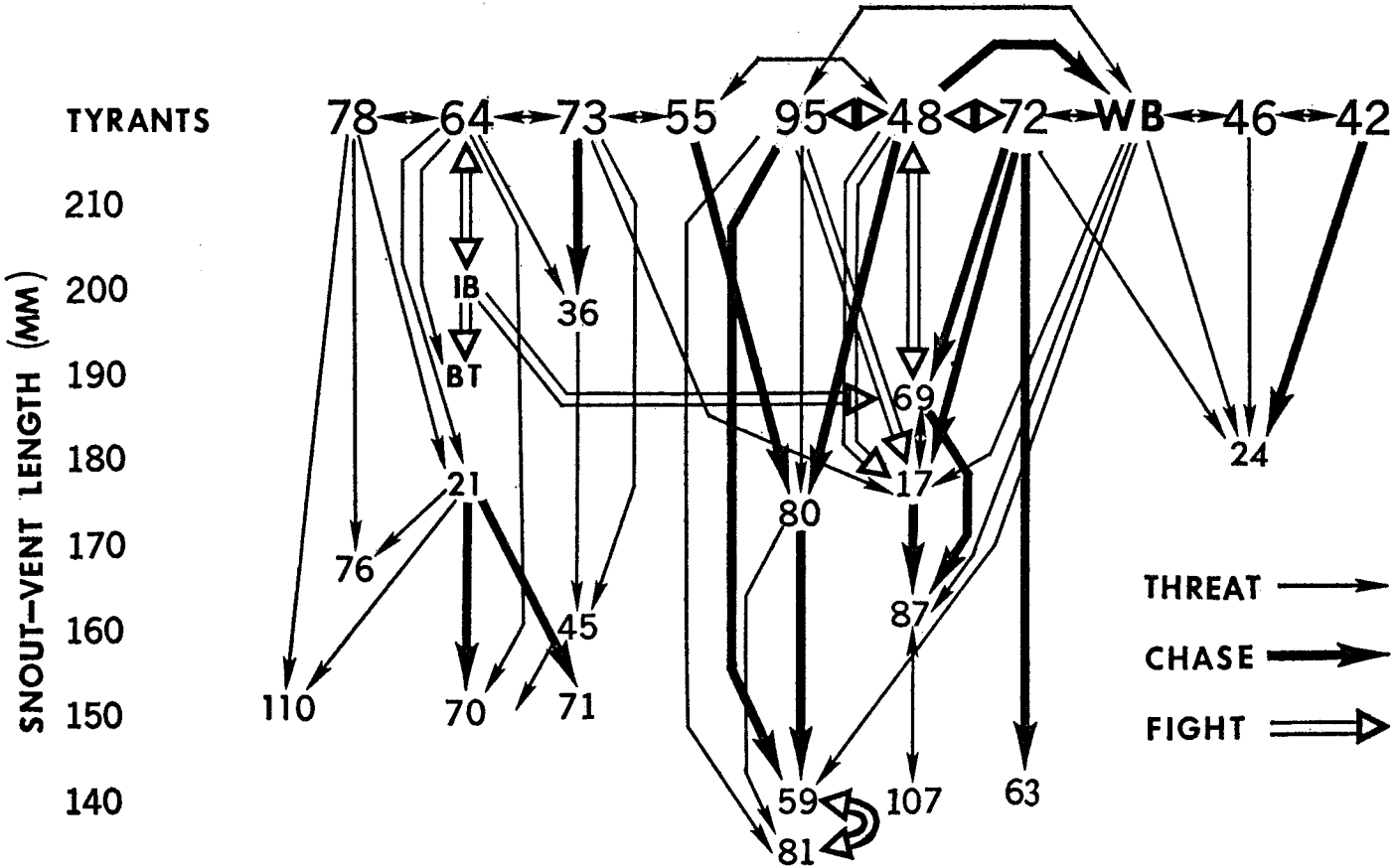

Fig. 15. Chuckwalla interactions within the dominance hierarchy at Lone Butte.

right angle to and facing IB. IB charged 69 again; 69 was still not inflated, the dewlap was withdrawn. The latter ran north, paused, did a few head bobs and reached the pink rocks (20 m from the initial combat site) at 12:11 P.M. The IB male continued to perform threat head bob displays at 69, 8 to 10 m away. The subordinate gradually moved north another 40 m, away from the tyrant. The tyrant left at 12:53 P.M.

Dominance Hierarchy

Tyrants and subordinate males of all sizes form a dominance hierarchy. Tyrants, the sole territory owners, top the hierarchy and have complete control within their territories. Subordinates within a given territory are subject to aggression from the tyrant, if he sees them. Most subordinates have home ranges that overlie two or more territories and as such can be intimidated and/or attacked by more than one tyrant.

Without exception the dominance hierarchy among subordinates is based on size. Larger lizards, using the techniques of threat, chasing and fighting, interact with smaller individuals who travel within their home range. Figure 15 depicts some aggressive interactions and inter-relationships of tyrants and subordinates. A tyrant does not allow a male of any size to remain within his territory if he sees him (there was one exception: see p. 46).

Territories have boundary lines that are real to the lizards. Presence of a subordinate a few dm inside the territory initiated aggression; whereas a lizard basking, feeding, or displaying outside the territory brought at most a threat display. Subordinates shuttle back and forth between territories and the free zones (areas with no territories) to avoid tyrants.

One intimidation, chase or fight between a subordinate and a tyrant did not appear to decrease the likelihood of a similar interaction occurring in the future. Although positions in the hierarchy were established in March and did not change as the season progressed, subordinate lizards constantly interacted with and tested those higher in the social structure. For example, two individuals, 69 and 17, were involved in numerous chases and fights (fig. 15). Both males initiated acts of aggression against tyrants and subordinates, but their social status remained the same after each encounter. Even when 48 disappeared, 69 did not fill the territorial vacuum or court 48's female.

Aggression Chains

Chains of aggression are situations in which a dominant lizard intimidates, chases or fights with a subordinate; and the loser, within a few minutes of the interaction, threatens and attacks a third and smaller lizard. Five aggression chains were noted in 1970 and 1971. Two chains involved 4 lizards and three chains had 3 lizards. All involved tyrants. In two additional interactions, a tyrant observed 2 lizards in a fight, then chased and fought with the winner.

A typical aggression chain occurred on June 6 at 9:45 A.M.:

Tyrant 55, who had been courting female 90, sighted male 80 about 30 m away and began to run at high speed toward him across the top of a dry waterfall strewn with boulders. Tyrant 55 pursued 80 for 40 m without pausing, twice leaping into the air as if trying to land on his back and ride him. At 9:49 both paused 8 m apart. Male 55 did several threat displays while 80 rested with mouth partially open and sides heaving (panting, fig. 8*j–k*), outside the tyrant's territory. At 9:50 A.M. the tyrant, after performing 2 more threat displays, headed back toward

the female courtship site doing displays as he traveled. About an hour later, at 10:46, the tyrant again charged at and chased 80 from a 2.5 m promontory in his territory. The tyrant displayed for about five minutes on the promontory and then left. Just as he departed, 80, who had run about 40 m, turned and chased 81 (an immature male) up a boulder strewn slope for 50 to 60 m, until the small lizard hid under a rock. The subordinate 80 did not perform threat displays either before or after the interaction with the tyrant or the immature male.

The Social Structure in 1970, an Exceptional Year

As noted previously, rainfall in the winter of 1969-1970 was below average. Food supply was low and the lizards were very inactive. Few head bob displays occurred, there was virtually no courting, and aggressive interactions were 15.6% of those in 1971. Lizards spent most of their time feeding in perennials.

A dominance hierarchy existed around one large boulder pile with several stair-step levels. Several sweetbushes or chuckwalla's delight bushes (*Bebbia juncea*) grew out of the crevices. These grew nowhere else in the study area. Chuckwallas favored these bushes with their sweet-smelling yellow flowers and would straddle tops of the bushes and snap off flower heads. Five males fought over the rockpile and the feeding site during May, when the bushes were blooming. Again position in the hierarchy depended on size. In 1971, when annuals carpeted the ground, chuckwallas rarely fed in the sweetbushes.

Female Aggression

Females were involved in very few aggressive encounters; none in 1969, 15% in 1970, 1.56% in 1971, or a total of 3.38% for 1969–1971. This may be due to either the abnormally low numbers of females in the population and the resulting reduced number of encounters, or to the lack of aggressive motivation in female chuckwallas in general (table 11). Females of the herbivorous species *Ctenosaura pectinata, Amblyrhynchus cristatus,* and *Dipsosaurus dorsalis* also rarely fight (Evans, 1951; Carpenter, 1966*a*; Norris, 1953). Female marine iguanas, *Amblyrhynchus cristatus,* fight only over nest sites.

Only 5 different female chuckwallas were involved in a total of 5 aggressive situations. Each time the larger female was dominant and appeared to be defending a preferred basking area or a small territory. In 4 cases, the large female suddenly appeared and chased the smaller away from one of the former's favored rocks. In the fifth case, the dominant was courted by a male when the subordinate arrived. The dominant threatened the subordinate with 2 head bob display sequences and the latter left (with the male). The dominant females involved were very large, ranging in size from 173 to 205 mm SV. However, there were several occasions where 2 females were in close proximity and no aggressive interaction ensued.

DISPLACEMENT BEHAVIOR

Displacement is behavior irrelevant to the context in which it appears and which derives from the conflict of two or more opposing tendencies. Displacement occurred in several chuckwalla interactions; there were 4 clear examples in 1971. A synopsis of such an incident follows:

April 10. Displacement was preceded by a chase and threat. Two tyrants and a subordinate were involved. At 12:28 P.M., tyrant 55 was sighted chasing subordinate 17 across open ground

in a free zone. They paused, inflated with dewlaps extended, and did threat and challenge displays about 1 m apart. A second tyrant, 73, whose territory lay to the immediate south, was 3 m away from 17 and outside his own territory. Tyrant 73 started to move toward 55 and 17 and then retreated south to a rockpile just inside his territory. Tyrant 55 moved away from 17 to the west toward his own territory and did threat displays.

At 12:31 P.M., 17 left his rock, did several threat head bobs, then ran away from both lizards a few meters. He was still in the "free zone." Both 73 and 55 were in the same positions at the edges of their territories. The three formed an equilateral triangle with the lizards at the corners and about 20 m apart.

Male 17, the subordinate, moved a little, then rushed 3 m toward 73, as if to attack or charge, then stopped abruptly. He ran again toward 73, then turned and travelled rapidly in a circle, and began feeding on flowers. He had headed upslope toward 73, acted as if he were going to attack (charge), then behaved as if he thought better of it (escape), and began to feed (displacement). In the meantime, 73 moved closer and did threat displays. At 12:46, 17 left the feeding area and moved back to the basking rock. Tyrant 73 continued to do threat displays.

COURTSHIP

Courtship was observed 215 times in the field from 1968 through 1971. Twelve courting situations were logged for 1968 (a fraction of the actual, as chuckwallas were not the main interest of study), 6 for 1970 and 196 for 1971. No field observations were made at Lone Butte in spring of 1969. However, one pair was seen courting at Pisgah Crater, San Bernardino County, California.

Participants.—With few exceptions, tyrants did all the courting. Females of all ages and reproductive conditions were involved. Seven of 12 tyrants had harems of 2 to 5 females; 5 males were observed courting only 1 female. I believe that harem size would have been larger if the sex ratio had not been so heavily skewed in favor of males (see p. 9). Twelve tyrants were observed to court 24 females, 4 of them unidentified. Eight females were less than 150 mm SV and were considered prereproductive. The remaining 12 varied in size from 150 to 205 mm SV and were potential egg layers.

Subordinate males were associated with females on 13 occasions in 1971 but actually courted in only 2. The first involved the 200 mm SV IB male, who courted prereproductive 58 and appeared to be paired with her. This male had all the attributes of a tyrant except territory. The other situation involved subordinate 80 and immature 60. Male 80 courted 60 from April 1 to April 28. By May 4, the female had moved into the territory of tyrant 55 and had become a member of his harem.

With the exception of the IB male, all subordinate males that were associated with females did few, if any, displays, and did not nudge, lick or rub their jaws on the females. In addition, after late April, subordinate males did not come in contact with females. Tyrants managed to patrol their territories frequently and threatened or chased any subordinate from the territory. I feel that a male without a territory would be unlikely to court or eventually mate with a female.

Harem and pair formation.—Although courting began in early March, females were apparently not committed to a particular tyrant or his harem until later in spring. As female home ranges extended over the territories of two or more tyrants, females could choose the tyrant. Situations where a female obviously exercised her choice occurred 3 times. In the first case female 61 was courted by and was in the close proximity of tyrant 48 from March 11 through 27. During

this time she travelled between his territory and that of an adjacent tyrant, 72. On March 28 tyrant 72 courted 61 for the first time. By April 1 the two had apparently formed a bond and 61 remained within the orbit of 72 for the rest of spring.

A second example involved a prereproductive female, 60, who was courted by subordinate 80 from April 1 through 28. Her home range in previous years had slightly overlapped the northern territorial boundaries of tyrant 55, who frequently intimidated and chased 80. During late April, the tyrant appeared within 30 to 40 m of her basking sites and displayed frequently. She gradually moved into the center of his territory, 100 m away, and became part of his harem.

The third case involved a female, 56, who was courted by and paired with male 48 from early March through April. Tyrant 48 disappeared in early May (probably killed; see p. 34). His female remained within the confines of his territory until May 16. During the 2 week period, 2 subordinate males frequented this territory but were not observed courting or attempting to court this female. She had a choice of 3 tyrants whose territories bordered those of 48 and also 2 subordinates. On May 16 she moved out of this territory and into that of tyrant 55 and was promptly courted by 55. She remained with 55 for the rest of the season.

Courtship Characteristics

Striking differences were noted in courtship techniques of pairs. The degree of participation and response of females varied considerably. Twenty distinct behavior patterns were noted; 6 occurred infrequently. They are defined and described below:

Nudging.—A male or female touches or nudges the opposite sex on the tail, at the tail base, hind legs or abdomen.

Licking.—A male or female licks the opposite sex. Sites most frequently licked include tail, tail base (cloacal area), hind legs, sacral region and dorsum.

Mate jaw-rub.—Jaw-rubbing involves a rolling motion in the horizontal plane in which the chin and side of the jaw are pushed forward and pulled back. The motion is frequently repeated three to five times. As the jaw moves forward, it is rotated so that the side of the jaw, cheek, and eye are rubbed on the return movement (fig. 16*b–d*). Sites that are jaw-rubbed include the abdomen, legs, tail, groin, dorsum, head, neck, and throat. Both sexes engage in jaw-rubbing.

Leaning.—The female rests her head and/or forearm on a part of the male's body, such as a hind or foreleg, abdomen or shoulder (fig. 12*d*).

Stroking and back clinging.—The female crawls over the back, tail and head of the male. She lies on his back, usually with her head resting on his head and forearms around his neck (fig. 12*c*). While lying on his back, she strokes his head and neck with her head and jaws.

Tunnelling.—The female nudges and pushes at the male's abdomen, groin, or axillary region with her snout and crawls under him, emerging at the opposite side of the abdomen, the throat, or between his hind legs and tail. Sometimes nudging or butting is energetic and the male loses his balance and falls off the rocktop.

Male walk over.—The male crawls over or stands over the back of the female.

Circling. The male and female move in a circle, head to tail, with the male nudging or licking the female. When nudged the female moves away and the male pauses to do courtship displays. He then walks forward to nudge the female again. While the male is displaying, the female may remain 3 to 7 dm in front of him or circle around and stand behind him. The two repeatedly exchange positions on rock or ground.

Pursuit.—A male or female pursues the opposite sex.

Male Pursuit Leap.—The male runs after the female, leaps into the air, and lands or attempts to land on her back while she is moving away from him.

Female Jerk.—The female, when nudged, licked or otherwise touched by the male, jerks and moves away.

Leaving.—One member of the courting pair leaves the other.

Licking the substratum.—A male or female licks the substratum, usually in the vicinity of or where the opposite sex has been.

Substratum jaw-rub. See mate jaw-rub, above.

Defecation.—See figure 16*e*.

Tail Twitch.—The tail is twitched back and forth horizontally in a vibrating, undulating manner.

Gape.—The jaws are opened and closed, as in a yawn.

Cloacal Rub.—The hindquarters and cloaca are rubbed on the substratum (fig. 16*f*).

Tail Arch.—The female lifts and arches her tail slightly, as if to defecate, but does not.

Hip Sway.—The hindquarters are swayed in a circular, rotary motion while the lizard stands with head, chest, and abdomen elevated off the substratum. The pelvic region may slightly touch the substratum (fig. 16*a*).

Defecation, tail twitch, gape, cloacal rub, tail arch, and hip sway each occurred fewer than three times during courtship. They are not considered an integral part of courtship.

Types of Courtship

Two distinct types of female participation and response during courtship were noted. The degree of female participation was based on size and age.

Type I.—Females smaller than 160 mm SV performed Type I courtship. There were 8 juveniles and immatures and 4 potentially reproductive females. Juveniles and immatures ranged from about 90 to 149 mm SV, the potentially reproductives from 150 to 154 mm SV. The latter group probably had not produced clutches prior to 1971.

Type I courtship involved extensive male to female physical contact. It consisted of nudging, clinging and stroking, tunnelling, and circling. During courtship females licked and rubbed their jaws on the substratum and on their mates. Less common behavior patterns included leaning, leaving and the female jerk.

Juveniles and immature females maintained more physical contact with males than the potentially reproductive females did. The former actively courted males by nudging, licking and rubbing their jaws on the bodies of the males; they also lay on the backs of males and stroked their heads and necks with jaws and snouts. Juveniles and immatures crawled under and over the males and often

lay on their backs with forearms extended around their necks and with head and throat resting against the neck for 30 minutes at a time. The males lay passively or stood in one position (fig. 8*e–f*). Males might perform head bob displays at intervals of 15 seconds to 2 or 3 minutes. Often the pair would walk in a tight circle, nudging each other, with either the female breaking away to climb onto the back or hips of the male or the male pausing to display. A synopsis of typical courtship follows.

April 1, 12:00 P.M. Tyrant 42 was basking on top of a boulder with head slightly elevated off the rock surface. Female 103 was lying on his back, her forearms around his neck and her head resting on his head. 12:25 P.M. The pair were in the same position. The forearms of the male were directed posteriorly and were pressed to his sides (fig. 8*c*). 12:26 P.M. The female moved forward on the tyrant's dorsum and sat on his back with her head and chest elevated. 12:35 P.M. The wind began to blow; 103 flattened out on 42's back with her head resting on his back. Then she crawled forward on his head and rubbed her jaw on his neck and licked his head. 1:07 P.M. 42 and 103 circled. 103 crawled up beside 42, rubbed the side of her jaw on his leg, pressed and rubbed her jaw on his abdomen. She tried to crawl under him. She rubbed her throat and then rested her throat on his abdomen. 1:10 P.M. Still in same positions. Tyrant 42 turned, nosed 103, then crawled over her and facing away, did head bobs. She rubbed her throat and chin on his sacral area, then crawled onto his back. She rested on his back, rubbed her jaw on his back and crawled off him. She circled around on the rock and came toward him, as he approached her. While she rubbed her jaws on his abdomen, he tried to lick her tail and cloacal area. She crawled underneath him and lay there, rubbing her jaws on the rock as he did head bobs. After emerging she nosed his tail base, rubbed her jaws on his thigh and crawled onto his back. 1:14 P.M. They circled. The tyrant rubbed his chin and head on her back, etc.

Larger females (150 to 160 mm SV) devoted less time to lying on the mate's back or crawling under him. Instead they often rested beside their mates with forearms draped across shoulders and with heads and necks resting on the heads or necks of the males (leaning). The increased mass of the larger females may render tunnelling and clinging awkward.

Type II. Females participating in Type II courtship ranged in size from 170 to 205 mm SV. The ♀ in this group rarely engaged in nudging, clinging and stroking, and tunnelling. Occasionally one would use leaning. Courtship consisted of circling, female jerk, and licking the substratum. Tyrants actively pursued these females, circling, licking the substratum and rubbing their jaws on the substratum. When nudged on the tail or tail base, the female might run .5 to 3 m away while the male paused to perform head bobs. For example:

May 16. Tyrant 55 basked on a rockpile a few cm from a vertical crevice from 7:45 to 8:25 A.M. At 8:25 female 56 emerged from the crevice, inflated. As he approached, she went back in. He did courtship head bobs. She partially crawled out as he did more head bobs. He circled around with dewlap extended and climbed higher on the rock above her. At 8:43 A.M. 55 moved up slightly on the rock and lay on a ledge 30 cm away. He did courtship head bobs and then approached her from behind. As he touched her tail with his snout, she jerked and moved away. He continued to approach, licking. He put a forepaw on her tail; she jerked and ran forward about 45 cm. He did head bobs at her former site and licked the area. With dewlap extended and chest inflated, he moved forward, paused and did head bobs. He lowered his head and moved forward, licking, crawled into the vertical crevice which she had occupied, as she lay above the opening. He emerged, faced her and did head bobs. When he walked nearer (30 cm), she moved away.

Two females, 61 and 29, bobbed in synchrony during or after male courtship

display (see pp. 28–29). Bobbing was a regular feature of courtship for these two and occurred only once with another female and her mate.

Tyrant 73 and female 29 courted in this manner:

April 29, 10:37 A.M. Female 29 was a few cm from 73 and was partially in a crevice. She crawled out and put a forefoot on his head. After emerging she moved her head from side to side in a horizontal plane, an action repeated later. (The reason for or function of this behavior is unclear.) Tyrant 73 did courtship displays. The two were about 3 cm apart, both facing the same direction. Male 73 moved around and rubbed his jaws at the base of her tail. As she moved away, he began bobbing and she joined in after moving about 20 cm, but they did not bob in synchrony. He walked toward her and rubbed his jaws on her tail base. When finished, she turned and they both bobbed at the same time but not in synchrony. He was slightly behind her and his forefeet were near her hindfeet. 10:47 A.M. 73 moved off the rock, circled around, came up beside 29 and did head bobs with dewlap extended. She did none. He turned to the south and displayed. She remained in the same position.

As noted previously, one female, female 56, lost her mate, male 48, and eventually joined and mated with another tyrant. Female 56 used a different courtship pattern with each mate. Although a large adult, 56 nudged, stroked and frequently rested her head, shoulders and chest on male 48. Her modified Type I courtship was the single exception among the large adult females. However, in May, after 48 disappeared, she moved into the territory of 55 and was courted by him. She then used Type II courtship, typical for females her size.

Copying Behavior.—During courtship either males or females may imitate or mimic the behavior of a mate. In 1970, a pair, female 56 and male 17, were observed together on May 21. At 2:00 P.M. the female watched the male approach her rock. Suddenly he climbed into a creosote bush and ate blossoms. At 2:01 P.M. he leapt out of the bush, travelled along the ground, pausing frequently to nose the substratum. When parallel and a meter from the base of 56's rock, he broke into a run and then stopped suddenly at the base of a burrobush and fed. She moved off her rock and ran after him, ate at the burrobush he had just vacated, while he climbed a rock next to the bush. Meanwhile the male left the rock and fed at another burrobush. When he left that site, she fed there also. This "copying" continued for 15 minutes, until the male disappeared. The female seemed more interested in the male than he was in her.

In 1971 two pairs exhibited similar behavior with regard to digging on three separate occasions. On March 30 female 1 went under a rock that had a mound of fresh dirt in front (as if a small animal had recently dug a hole under the rock). She dug for a minute or so, emerged, and climbed on top of the rock. The male who had been pursuing and attempting to court her, imitated this behavior. He went underneath the rock and dug with his forefeet, kicking dirt with his hind feet. When he came out, she again disappeared under the rock and dug again, while he did head bobs on the rock top. He imitated her again and then both fed on wildflowers.

MATING

Three matings were observed in the field on June 5, 6, and 8 and two more in the outdoor pen on June 13, 1971. The three matings at the study site involved tyrants and females who courted regularly throughout the spring.

Courting activity showed an increase in pursuit and the male pursuit leap

in the last week of May. Females, in turn, tended to leave the courting site and jerked and moved away when nudged or licked. The first observed mating attempt occurred on May 23 when tyrant 55 twice leapt unsuccessfully onto the back of female 90. During the second attempt, she fell into a can trap.

The five matings had three similarities: all females involved were adults (160 to 205 mm SV); copulation lasted from 3 minutes 50 seconds to about 6 minutes; and all matings took place on the ground, on soil or loose talus between large rocks or boulders. There were also significant differences. Each mating is described to show variation in behavior of the prenuptial response and degree of participation.

The first occurred on June 5 at 10:35 A.M. between tyrant 46 and a 160 mm SV unidentified female, whom he had courted since March.
There was no foreplay or warning:

10:20 A.M. The tyrant was courting a small, immature female. The two were on top of a 1 m boulder. The female was using Type I courtship techniques and was nudging the tyrant's tail base, crawling under and over him, stroking his sides. They circled and he performed courtship displays. At 10:34 a larger female appeared suddenly at the rock base. Tyrant 46 left the small female on top of the boulder and quickly moved down the side of the rock to the second female. The two circled rapidly several times. Just before he mounted her, they were facing opposite directions with the male on top of the female. The head of the male was over the pelvis of the female with the female's head under his abdomen. He rubbed his chin horizontally back and forth on her sacral area. He grabbed her first on one side of the cheek and then the other. She did not try to escape. The female lifted her tail as the male wrapped his around the base of hers. Copulation lasted 3 minutes and 50 seconds. The small female disappeared sometime during copulation, and the mated female left immediately afterwards. The male climbed to the rocktop with his tail arched and did 2 head bob displays. Rubbing of the jaw on the sacral area of the female did not occur again in the later matings and foreplay was always present.

On the same day tyrant 55 attempted to mate with female 1 from 9:30 A.M. until at least 12:30 P.M. when field observations were terminated. Each time he succeeded in landing on her back after a brief run and leap, the female crawled under a rock or into a vertical crevice and rubbed him off. He spent much time in the crevice and under the rock nudging and licking her. Between mating attempts he waited on a rocktop 3 to 4 m away for her to emerge, ignoring a smaller female and member of his harem who watched a few meters away. When 1 came out of the crevice, he immediately dashed over to display and to pursue her. The two were still in the same places the next day, on June 6, at 9:25 A.M. Tyrant 55 continued the same kind of courting procedures, with a few minutes out on several occasions for aggressive action against subordinate male 80. At 12:55 P.M. he entered a rockpile doing head bobs and disappeared from view. He was pursuing female 1.

12:57 P.M. Tyrant 55 and female 1 emerged together from the rock. 55 was mounted on 1 and had a piece of neck skin (immediately posterior to the parietal eye) in his mouth. They remained in this position for 55 seconds, until the female jerked. Then 55 wrapped his tail under hers. At 1:01 the male's body jerked spasmodically about 5 times. He gulped air, then bit her again, released her. As she pulled free, he arched his tail and did head bobs at 1:02 P.M.

The last mating in the field involved this same tyrant and female 56. They were observed at 8:29 A.M. circling together, with 55 nudging 56. She jerked

and moved away 30 to 50 cm but frequently came up behind him as he displayed. They were coupled from 8:39 to 8:45 A.M. The tyrant remained with the female after they mated. They moved about 70 m to a large rockpile with a horizontal crevice. He continued to circle and head bob with her, twice crawling onto her back but not attempting to bite or mate. She entered the crevice at 9:13 A.M. and did not emerge again that morning. He remained with her, basking and displaying above the crevice.

The pen matings present quite a contrast. Little if any courtship similar to that described for the field was observed, and the subordinates copulated with the 2 females. Five chuckwallas, 3 males and 2 adult females had been kept together since early April. A third and smaller female was present for a few weeks in May. The males formed a dominance hierarchy based on size.

On June 13, while the tyrant was fighting with the Black Striped male, the White Shouldered male (smallest) mated with a female. In late afternoon the tyrant was eating lettuce from my hand when the Black Striped male suddenly mounted and mated with the second female. Both matings lasted about 4 to 4.5 minutes and both occurred out of view of the tyrant. My presence within the pen may have distracted the tyrant.

THE TYRANT AS AN INDIVIDUAL

Each tyrant was unique in his method of territorial defense and courtship. Some tyrants used only threat and intimidation to maintain territorial boundaries, whereas others chased and fought with subordinates (fig. 15). Some courted females with "patience" and "finesse," whereas others appeared to be "clumsy" and uninterested.

Variations in Aggressive Tendencies

Tyrant 73, who courted one large adult female, female 29, used threat and intimidation exclusively to maintain his territory. He was the least aggressive of the tyrants and was not observed to chase or to fight another male. He allowed the subordinate 36, who was the former mate of female 29 and the former owner of the territory, to lie 20 m away from him and within his territory on numerous occasions. The subordinate usually assumed a "hidden" posture or lay with head slightly elevated (fig. 11*a–b*), while watching 73 court 29. The subordinate rarely sat up on the rock (fig. 8*f–g*).

In contrast, tyrants 64 and 55 used the chase more often than the threat. On several occasions these males observed subordinates basking on rocks within their territories at distances greater than 60 m. They charged at and chased the subordinates from their borders.

Variations in Courting Techniques

The more aggressive males had the larger harems. (Harem size did not appear to be related to quality or size of territory.) Male 55 had five females, 64 had three or four, and 72 had three. Tyrant 55, who had the largest harem, was very successful at courtship. He sat next to and displayed at the large adult females. When pursuing one, he usually paused 30 to 50 cm behind and did not leap

onto her back. He used the pursuit leap only when attempting to mate in late May and early June. Male 55 also visited all females in his harem once or more per day (on days observations were made), and only left the females to feed or for aggressive encounters.

Tyrant 72, who courted with a pursuit and pursuit leap style, appeared to lack patience and "finesse." He chased 2 of his 3 females with vigor, sometimes for 50 to 100 m. He attempted to jump onto their backs early in spring and often sent them scurrying into crevices. During May and early June his attention was focused on the largest of his females, a 200 mm SV adult. He did not visit the others in his harem frequently at that time.

One tyrant, the White Back (WB), was observed courting on 3 occasions only. His courtship attempts could be described as "half hearted." Once he appeared to be uninterested in the female and only tolerated her advances:

May 12. 10:35 A.M. A female (100–120 mm SV) courted the WB male. She crawled onto his back, rested inflated there, then moved forward. He jerked his shoulders, as if she were an irritation, and moved out from under her. He did 2 head bob displays facing away from her. She circled around behind him, crawled onto his tail and rubbed her jaw on his tail and sacral region. She rested on his tail and hips with her forearms posterior to his hind limbs, then tried to crawl onto his back. He moved out from under her and did head bobs with dewlap extended. She moved about 15 cm away, then returned, rubbed her head on his head and neck, crawled over his back and shoulders. He shook her off, then tried to nudge her with his snout. She crawled underneath his tail. He walked around behind her, licking, and tried to lick her tail base. While he did head bobs, she rubbed her jaws on the rock, his tail and hind leg, and tried to crawl under his hind leg and tail. She rubbed and stroked his abdomen, crawled out the other side and tried to crawl onto his back. 10:40 A.M. He went over the east side of the rock and disappeared. 10:42 A.M. He returned, rushed in from the south toward the female. They circled, he faced away and did head bobs. She crawled onto his back and rubbed his head. He shook her off by twitching shoulders and head. She came up behind and rubbed his vent with her chin, then moved onto his back, placing her forearms on his head. He made a circle, shaking his head and shoulders before getting her off, then did head bobs. He finally left her.

PREDATORS

Several avian, mammalian, and reptilian predators of chuckwallas occur at Lone Butte. Predatory birds include the golden eagle (*Aquila chrysaetos*), red tailed hawk (*Buteo jamaicensis*), raven (*Corvus corax*) and road runner (*Geococcyx californianus*). Coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*), and bobcats (*Lynx rufus*) are common in the area. The spotted skunk (*Spilogale putorius*) and badger (*Taxidea taxus*) occur here but were not observed at the study site. Lizard-eating snakes such as the glossy snake (*Arizona elegans*), gopher snake (*Pituophis melanoleucus*), kingsnake (*Lampropeltis getulus*), patched nose snake (*Salvadora hexalepis*), coachwhip (*Masticophis flagellum*) and sidewinder rattlesnake (*Crotalus cerastes*) are potential predators on hatchling and young chuckwallas. Two other likely predators, the Mojave rattlesnake and speckled rattlesnake, are found here but were not observed.

On 16 occasions (0.287/obs. hr) chuckwallas responded to gliding and soaring birds. Twelve of the 16 interactions occurred with ravens. The other 4 involved a LeConte's thrasher (*Toxostoma lecontei*), mourning dove (*Zenaidura macroura*), a red tailed hawk and a turkey vulture (*Cathartes aura*). Responses of chuckwallas to these birds ranged from: assuming an alert posture and jerking

of the head from side to side; to shifting to a "hidden" posture (fig. 11*a–b*); to flight, followed by a return to the basking site within 1 to 5 minutes. Distances of the birds from the lizards were difficult to estimate accurately.

In general, the closer the gliding or flapping bird, the more likely the chuckwalla was to flee. Several times three to five lizards fled with the appearance of the hovering bird, but others in the vicinity did not. If the bird cast a shadow near a chuckwalla, the lizard usually ran away. The interactions with the LeConte's thrasher, mourning doves, and turkey vulture involved juvenile lizards and in these instances the lizards fled.

On June 23 and July 20, 1971, a coyote walked through the study area. Both times all the lizards sighted the coyote before I did and all immediately fled into crevices. Three lizards were under observation in the first case and 5 in the second. The second time one juvenile emerged 24 minutes after the coyote left, but the others did not come out again that morning. The coyote alternately walked and trotted through the area, often pausing to sniff a rockpile or look into crevices.

Coyotes are known to feed on chuckwallas. Howard Leech of the California Department of Fish and Game found parts of chuckwalla feet in coyote scats taken from Borrego State Park, San Diego County, and Harpers Flat on November 28, 1954 (Stebbins, 1955). Three coyote scats containing chuckwallas were found five miles east of the study area in 1972. Five of 500 preserved chuckwallas in museum collections had lost feet and/or legs. Two were missing two feet, one forefoot and one hindfoot. In all cases the stump had healed over. Male 36 at Lone Butte was missing the left foreleg. Mammalian predators, coyotes in particular, may be responsible for such mutilated limbs.

COMMUNICATION BY CHEMICAL SIGNALS

Burghardt (1970) recently reviewed evidence for chemical perception in reptiles. Prieto (1972) studied the responses of chuckwallas to various species of snakes. Although no controlled experiments were run to determine abilities of chuckwallas to detect various odorants, the behavior of the animals in the field indicates that chemical signals are a source of information and an important means of communication.

Detection of Signals

Males and females of all sizes frequently lick the substratum. When travelling, the lizard pauses every 30 to 50 cm to lick sand or rocks. Before entering a crevice that has not been used for a few hours or days, the lizard licks the entry and ventral edges several times per minute and may continue licking for five or more minutes. Certain lizards, when entering a new area or place infrequently visited, explore under rocks and in crevices. They lick frequently.

Courtship and aggressive behaviors involve licking. During courtship, licking the substratum and the opposite sex were the two most frequent behavior patterns. Twice, intensive licking followed defecation:

May 25, 1969. Pisgah Crater, San Bernardino County. 9:15 A.M. A male and female were sighted 100 m apart. Between 9:15 and 9:45 the male travelled toward the female, pausing to perform head bobs. 9:46 A.M. The male arrived at the female's rockpile and did courtship

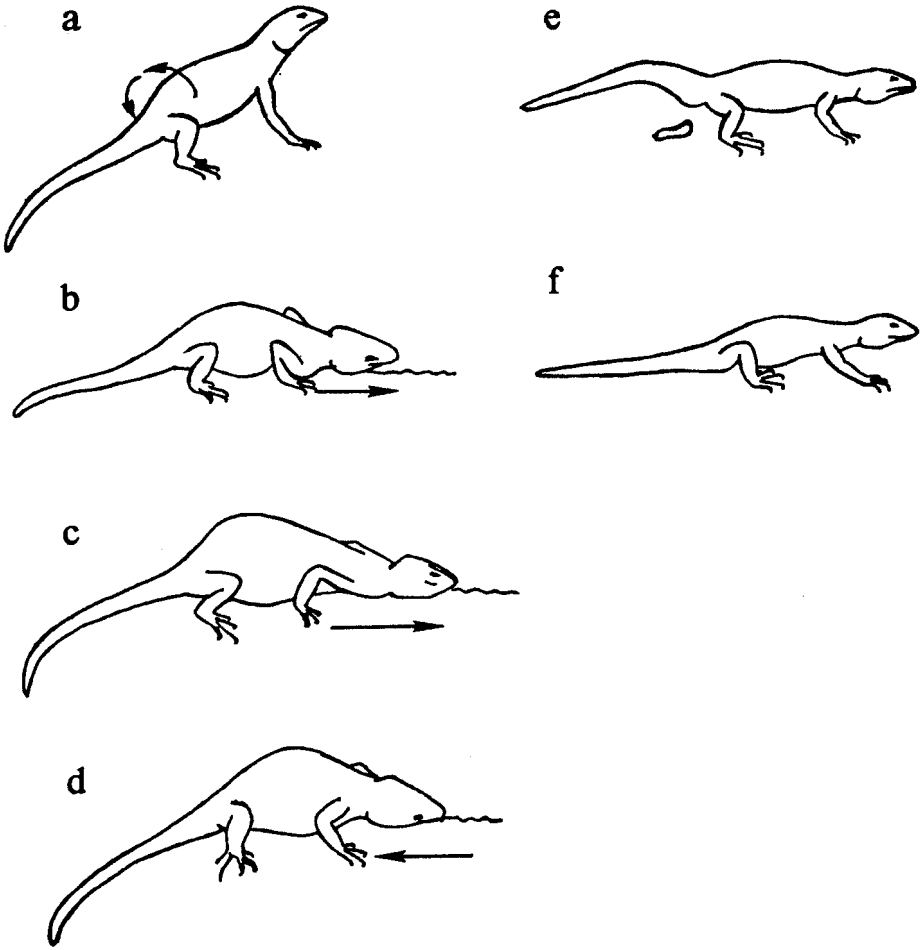

Fig. 16. Chuckwalla postures used in possible deposition of chemical signals: *a* hip sway; *b–d* rubbing the jaw on the substrate; *e* defecation; and *f* tail wipe.

head bobs. She circled around behind him, climbed over his back, and paused behind him. 9:52 A.M. She defecated, lifting her tail. Her cloaca appeared to touch the rock. He licked the rock where her cloaca had rested, licked the dropping and the rock several times. He licked her cloaca.

April 23, 1971. Lone Butte. The IB male and immature female (58) had been courting since 12:35 P.M. 1:30 P.M. The IB male lifted his tail, defecated and rubbed his cloaca and hind quarters in a dragging motion on the rock (fig. 16*e–f*). The female, who was behind him, rubbed her jaw on the rock and circled around. IB moved forward a few cm and did head bobs while she crawled over to him. She rubbed her jaws in the area where he defecated. She continued to lick the substratum and rub with her jaws for 45 seconds or so, then circled on the rock. He remained in the same position 30 cm away.

Licking occurs after aggressive encounters, especially if a dominant displaces a subordinate from a rock promontory. The dominant alternately licks the site that the subordinate vacated and performs threat displays.

Licking is probably a method of detecting chemical signals placed on the substratum by conspecifics and/or ophidian predators.

Deposition of a Chemical Signal

Chuckwallas may mark an area by: rubbing the jaw on the substratum; rubbing femoral pore secretions on the substrate; defecation; urination; cloacal wiping; and the hip sway.

Rubbing the jaw on the substratum (fig. 16*b–d*) is a common behavior pattern and occurs during courtship, aggression and when the lizards are apparently solitary. In one courtship situation, adult male 73, who was courting female 1, jaw-rubbed and left the rock. The female immediately ascended the rock and jaw-rubbed in the same place. There may be scent producing glands associated with jaws or eyes.

Femoral pore material is a possible territorial marker. It may also produce an odor that facilitates pair formation in spring (Cole, 1966). So far this has not been demonstrated. Femoral pores in chuckwallas are strongly sexually dimorphic, being well developed in males and virtually absent in females.

Licking of fecal material suggests that scent glands or chemical signals may be associated with the cloaca or excretory organs. Again this requires further study.

DISCUSSION

The chuckwalla, *Sauromalus obesus,* is an iguanine lizard thought to be derived from ctenosaur stock. Ctenosaurs, as well as the other large herbivorous iguanines, are tropical and subtropical lizards. *Sauromalus* represents the northernmost extension of the iguanine line and is the only large saurian herbivore found in the temperate zone. During the Eocene its geographic distribution extended further north, into Wyoming, but with the drying trend the lizards have retreated south (Avery and Tanner, 1971).

The behavioral and life history characteristics of *Sauromalus obesus* indicate strong subtropical affinities. Although a desert dweller, it has managed to survive by evading desert-like conditions.

The Chuckwalla as a Specialist

The chuckwalla is a specialist. Living in a fluctuating environment, it is adapted to one phase and tolerates or avoids the other (Levins, 1968). In California, for example, the chuckwalla is adapted to the desert spring; it tolerates the summer by reducing metabolic expenditure (Nagy, 1972), and hibernates in fall and winter. These lizards are above ground only five to six months of the year, from late winter through the summer. Two to three of the dry summer months are spent in greatly reduced activity and food is unavailable. During summer chuckwallas can be found only with effort and are essentially in hibernation.

During a dry spring when food sources are limited (as in 1970), chuckwallas conserve energy by behavioral and physiological means. They are virtually inactive, performing few displays, doing little travelling, and only rarely interacting in courtship and aggression. Growth and reproduction are curtailed. Even with reduced activity, Nagy (1972) found that chuckwallas entered hiberation in 1970 weighing two-thirds of what they weighed in early spring, when they emerged from hibernation.

The way of life of a chuckwalla is that of an opportunist and a specialist, an animal geared essentially for a 4 month year in a year when food is plentiful.

Life History Strategy of the Chuckwalla

Chuckwallas are large, long lived, slow to mature, single brooded, and have repeated reproductions. Reproductive potential and recruitment rates are low. Populations in a natural environment are probably at or near carrying capacity. Thus chuckwallas have the life history and reproductive characteristics of an organism that has been selected to operate at environmental saturation or carrying capacity (the "K" strategist: MacArthur and Wilson, 1967; Pianka, 1970 and 1972; Hairston, Tinkle, and Wilbur, 1970). One might expect that the chuckwalla, living in an unpredictable, harsh environment, might find keen competition from a lizard that has rapid development, an early maturation, multiple reproductions and small body size (the "r" strategist: Gadgil and Bossert, 1970).

The herbivorous feeding mode may present additional problems for a desert dweller. Sokal (1967) has suggested that chuckwallas are inefficient herbivores and appear to have few specializations for herbivory. Cellulytic gut symbionts are absent and only volume, the relatively large body size, and sheering teeth compensate for inefficient food utilization. Availability of forage in the southern Basin and Range desert is unpredictable. Large quantities of suitable forage are present only in a spring following average or above average winter rainfall. Chuckwllas must be adapted to utilize food when it becomes available and to withstand long periods without it.

The short season and unpredictable food supply account partially for delayed maturity. One might predict rapid growth rates and earlier maturation in areas where food is more plentiful and readily available for longer periods. Indeed this is probably true of populations in the Sonoran desert of Mexico. However, no matter how much a chuckwalla eats, it would be unlikely to reach maturity until two to three years after hatching.

Females have much slower growth rates than males. The reasons for slow growth prior to sexual maturity are unknown, but the marked reduction in growth after maturation is probably associated with the large amounts of energy required for reproduction. Females require five to six years to reach maturity whereas a male may attain sexual maturity after about three years. However a male is not likely to take part in courtship or reproduction until much older and larger, about six to seven years. So that, although maturation periods are different, the two sexes may contribute offspring to the population at about the same time after hatching.

Chuckwallas have a reproductive strategy typical of a large, long-lived lizard (Tinkle, Wilbur and Tilley, 1970). They have an average clutch size greater than that of early maturing, multiple brooded lizards (4.27 for early, 6.48 for late, and 7.8 for chuckwallas). In addition, fecundity increases with age.

Tinkle (1969) suggested that as life expectancy increases, reproductive frequency decreases. In long-lived species, selection favors individuals that put less energy and resources into reproduction per season, especially if fecundity increases with age. Such a strategy increases the probability of lifetime success.

Chuckwalla reproduction follows this pattern. It is erratic and is dependent on winter rainfall and food supply; eggs may be laid only when vegetation is abundant and even then not all mature females lay. Egg production is risky in the desert; by the time eggs are laid, annuals and perennials have dried up for the season. Females have expended fat reserves and are spent; they may find survival through the dry summer and winter hibernation very difficult. Tinkle (1969) found that the probability of living to another reproductive year is inversely proportional to total fecundity during each breeding season.

Sex Ratios and the Lone Butte Population

Sex ratios at Lone Butte show a predominance of males. Fewer females may be recruited to immature and adult age classes and mortality at all levels may be greater for females than males.

Natural selection usually produces a 1:1 sex ratio. The mechanisms for this have been discussed by Kolman (1960), Leigh (1970), Emlen (1968), Verner (1965), and Willson and Pianka (1963). Contradictory views on the effects of mortality on the primary sex ratio have been presented by Emlen (1968) and Kolman (1960). Andersen (1961) has dealt with the relationship of density and sex ratio, and Hamilton (1967) reviewed extraordinary sex ratios, sex linkage, and inbreeding.

The imbalanced sex ratio at Lone Butte could be caused by a skewed ratio at hatching; alternating wet and dry years which stress females in reproductive condition; and high population densities with the weaker animals suffering greater mortality. The sex ratio at hatching is unknown.

Drought is not a new feature to the desert or to a chuckwalla. There have been three major droughts in the last century alone and one conceivably within the life time of large adults at Lone Butte. The Argus Range also receives below average rainfall at least every three years, so the population experiences regular dry periods on a smaller scale. I do not feel that dry conditions alone contribute to sex ratio imbalance.

Johnson (1965) reported an almost equal sex ratio in a population near Lone Butte; the density of this population was much lower than that at Lone Butte. The combination of high density, unpredictable rainfall, and heavy metabolic demands of egg laying may stress the adult females and result in higher mortality. This could account for the skewed sex ratio of adults but not for the low recruitment in the immature age class.

Chuckwalla Displays

Chuckwallas communicate via head bob displays, postures, and possibly odor, or in combination. Chuckwalla displays are unique among lizard displays so far investigated: each animal appears to have its own pattern, the "signature," which has remarkable constancy and little variation within the individual. Most head bob displays are performed by adult males who are dominant or close to the top of the social hierarchy. Displays are used to intimidate or to threaten other males or to court females.

"Signature" displays may be used for individual recognition. Long-lived lizards

with a complex social structure that includes both a territorial system and a dominance hierarchy may know individuals within their home range and recognize them by the "signature" displays. Individual recognition could conserve energy and reduce the number of aggressive encounters. Tyrants often see subordinates at distances of 100 m or more and will run over to them and threaten, chase or fight with them. Subordinates can avoid the displaying tyrants and especially the tyrants that are likely to chase or fight with them.

The same "signature" display is used for courtship and for aggression. This is an example of a hostile display that is also important in pair formation and may be compared with the songs of passerine birds.

Moynihan (1955), in a study of hostile displays, suggested that unmated females may recognize sexually motivated males by their performance of certain typically masculine and hostile reactions, such as displays "advertising" possession of territory. The displays may be attractive to females and may even have a stimulating effect upon female sex drive. Moynihan (1955) remarked that the stimulating effect has not been proved to operate in any animal. I believe that the male threat displays may have this effect on the prereproductive chuckwalla females. Certain young females did join a displaying tyrant at his basking site.

Infrequent use of assertion or aggressive displays among females may be significant. Adult male chuckwallas, especially tyrants, are very aggressive and readily respond to displays of other males inside or outside their territories. A displaying female might attract a male and stimulate hostile behavior.

Social Structure

The social structure of *Sauromalus obesus* encompasses both a territorial system and a dominance hierarchy at one locality. Hunsaker and Burrage (1969) have postulated that territorial situations occur when populations are in low densities and individuals can maintain individual distance by retreat. A social hierarchy is formed when density is high and retreat impossible. Brattstrom (1971) experimentally manipulated groups of the bearded dragon, *Amphibolurus barbatus,* in pens and obtained territories at low densities and social hierarchies under crowded conditions. Stamps (1973) found variable social systems in wild populations of *Anolis aeneus.*

The Lone Butte chuckwalla population had a large number of sexually mature males but only 12 were observed to hold territories. The rest of the male adults and the immatures were aligned in a dominance hierarchy. Possession of a territory provided the tyrant with at least three selective advantages. First, a tyrant had one or more females within his territory and courted them exclusively; other males did not have an opportunity to court with these females. Second, a tyrant could utilize all the food resources in his territory, whereas a subordinate could feed only in the free zone or in a territory when the tyrant was unaware of his presence. Third, the tyrant had "first choice" of protective cover (rock crevices).

Rand (1967) suggested that territories are defended when there are selective advantages for control of environmental resources and mating and for protection and survival of offspring. Control of environmental resources and mating

were advantageous to the tyrants, but chuckwallas are not known to provide maternal care or to protect the offspring.

Aggression

Chuckwalla males were highly aggressive. They not only used ritualized threat displays but also chased subordinates for 50 to 60 m and would attack. Fighting was ritualized (formalized sparring match with a stereotyped behavior pattern) but could also be overt (a fight to the death with nothing barred; Matthews, 1964). Most animals use ritualized fighting and deaths from fighting seem rare in natural situations.

There was a constant state of aggressive tension at Lone Butte during the breeding season in 1971. Animals of lower social rank were continually infringing on territories of their superiors, arousing hostility in the form of threats, chases, and fights. Matthews (1964), in a review of overt and ritualized aggression, reported that wild animals do not live "in a state of emotional tension." The dominant animal takes first place but is not forced constantly to hold his position through hostile acts. However, chuckwalla tyrants were repeatedly tested by subordinates and constantly patrolled their territories, defending them from lower-ranking individuals.

The Lone Butte population may exhibit abnormally high densities. A high density could account for the extreme degree of aggression, as well as the imbalanced sex ratio.

Courtship

Chuckwallas are polygynous but not promiscuous. A tyrant forms a bond with a female that lasts for three and a half months, but the bond may be maintained for several years. The tyrant courts each female in his harem almost daily from March through May but mates only in late May or early June.

Lorenz (1967) has suggested that bond formation occurs only in species that are highly aggressive. Male chuckwallas were highly aggressive; females were not. A tyrant might form bonds with females as a means of keeping them within the territory until mating in late spring. Because females do not produce clutches every year, bonds of greater than one season in duration insure greater chances of a tyrant's contribution to the gene pool. The female, in turn, produces a clutch sired by a dominant male.

The role of the immature female in courtship is puzzling. Prereproductive females appeared to seek physical contact with males and solicited their attentions, whereas large, mature females avoided physical contact. There may be at least two reasons for the behavior of immatures. First, by pairing with a tyrant, an immature female may avoid hostile encounters from him and from subordinate males. The clinging, stroking, and tunnelling may be a form of deceptive display which reduces the aggressive drive of the male by stimulating nonhostile or sexual activity. Second, the female may stimulate sexual development, courtship and/or mating in the tyrant through the extensive physical contact of stroking, clinging, tunnelling, and jaw rubbing. The behavior of tyrant 46 prior to mating with an adult (see p. 45) is of special interest here. The tyrant was courting a prereproductive female when an adult suddenly appeared. He imme-

diately approached her and they mated with no foreplay. The young female could have "prepared" the tyrant for this mating. The young female does not receive immediate "gain" by such activity. However in future springs she may pair and mate with the tyrant.

The chuckwalla has a complex social system, a combination of territories and a dominance hierarchy, both polygyny and pair formation, and elaborate and prolonged courtship. The complex social system, which appears to be activiated only when environmental conditions are suitable for reproduction, may help to insure survival in a harsh and unpredictable environment.

SUMMARY

The chuckwalla, *Sauromalus obesus,* is an herbivorous, rock-dwelling lizard that lives under rigorous conditions in the southwestern deserts. It is large, long lived, slow to mature, single brooded and has repeated reproductions. Its reproductive strategy is typical of a long-lived lizard. The Lone Butte population had low reproductive potential and low recruitment. Most lizards were adult, and few juveniles were added each year. In some years none appeared.

Female chuckwallas may have lower survivorship than males. They grew more slowly than males and required about twice the time to reach sexual maturity. In addition, the sex ratio was strongly biased toward males with fewer adult and immature females than males. Adult female mortality may be due to heavy metabolic demands of egg laying in a harsh environment. Since suitable forage is gone when oviposition occurs, a spent female may be unable to survive the dry desert summer and hibernation the following winter.

The chuckwalla is a specialist and opportunist, adapted to the desert spring in a year of average or above average rainfall. Seasonal activity patterns differed markedly between 1970 and 1971. 1970 was a year of low rainfall; few annuals bloomed and perennials produced few shoots or blossoms. Lizards did few head bob displays, little courting, had few aggressive encounters, and moved infrequently. In 1971, when rainfall was about average, the desert was carpeted with flowers. Lizards displayed, courted, and mated. Aggression and travelling were frequently observed. Eggs were laid in late spring and summer. During dry periods, chuckwallas survive through inactivity and reduced energy expenditure. When rainfall is adequate to produce suitable forage, they reproduce.

During summer, chuckwallas are inactive. They emerge to bask, but not daily, and feed and travel infrequently. In fall they hibernate.

Social structure was controlled by large adult males, the tyrants. Tyrants communicated with each other and with other chuckwallas by postures, head bob displays, and perhaps chemical signals. Chuckwallas perform a single basic head bob display, "the signature," which differs for each lizard but is remarkably invariable and consistent for an individual. It may be used in species recognition. Head bob displays are used to advertise territory, to threaten, and to court. Most displays are performed by tyrants or other adult males.

A territorial system and a dominance hierarchy existed in the chuckwallas studied. Only tyrants held territories, which they actively defended by threat displays, chasing and fighting. Subordinate adult and immature males were

aligned in a dominance hierarchy. Because home ranges overlapped considerably, there were several subordinates living within each tyrant's territory. Subordinates travelled from one territory to another under constant threat of attack from the tyrants. Few "free zones" not defended by tyrants existed.

With few exceptions tyrants did all the courting and mating. A tyrant had one or more females within his territory and courted her/them from March through June. Mating occurred in late May and early June. Tyrants may be polygynous but were not promiscuous. Each assiduously courted each female in his harem on an almost daily basis, apparently forming a pair bond.

Courtship was elaborate but varied with a female's size and age. Prereproductive females or those that had just attained sexual maturity nudged and stroked the males with their snouts, crawled under and over them and lay on their backs for several minutes at a time. However, the large adult females, who had probably laid more than one clutch, did not seek physical contact with males. Instead they jerked and moved away when the males approached to nudge and lick. Although these females licked and rubbed their jaws on the substrate, they infrequently touched the males.

The complex behavior and social system of the chuckwalla may help to insure survival in a rigorous environment.

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