Life history and ecology of the Great Basin sagebrush swift, *Sceloporus graciosus graciosus* Baird and Girard, 1852

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LIFE HISTORY AND ECOLOGY OF THE GREAT BASIN SAGEBRUSH SWIFT, SCELOPORUS GRACIOSUS GRACIOSUS BAIRD AND GIRARD, 1852

by

Gary L. Burkholder
and
Wilmer W. Tanner
LIFE HISTORY AND ECOLOGY OF THE GREAT BASIN
SAGEBRUSH SWIFT, SCELORPORUS GRACIOSUS GRACIOSUS
BAIRD AND GIRARD, 1852

by
Gary L. Burkholder1 and Wilmer W. Tanner2

INTRODUCTION

The sagebrush swift, Sce1oporus graciosus graciosus, is the most abundant reptile in the transitional zone of the Great Basin. In this habitat, being preyed upon by larger vertebrates and, in turn, preying upon arthropods, it serves as an intermediate link in the food chain. Previous ecological studies have dealt only with isolated aspects of the sagebrush swift's natural history. This study was undertaken to consolidate and to add to our knowledge of this species.

The sagebrush swift is found in western North America, from northeastern Washington and west central Montana south to northern Arizona, New Mexico, and southern California and from eastern Wyoming to the coast of northern California. Populations are also found in southern California, Baja California, western Texas, and southeastern New Mexico (Stebbins, 1966). One specimen was among those collected by the Stansbury Expedition to the Valley of the Great Salt Lake in 1849; this specimen was sent to the U.S. National Museum, where it was described by Baird and Girard in 1852.

Stejneger (1893) reported S. g. graciosus to occupy sagebrush areas at 2,450 m elevation in the White and Inyo mountains on the border of California and Nevada. In 1912 Taylor observed that Nevada populations were mainly ground-dwellers occupying sagebrush and pinyon-juniper plant associations. He also noted predation of sagebrush swifts by Crotophytus viridizii. Richardson (1915) made a survey of reptiles of northwestern Nevada and adjacent territory and found considerable morphological variation between populations. He noted that sagebrush swifts were abundant on low, sparsely forested moraines among Artemisia tridentata, Arctostaphylos sp., and Ceanothus sp.

More recently, Woodbury and Woodbury (1945) observed courtship behavior and gonadal cycle. Stebbins (1944 and 1948) and Stebbins and Robinson (1946) studied territoriality and longevity in northern California populations of S. g. gracilis.

The stomach contents of graciosus in Utah were analyzed in studies by Pack (1921), Gertsch and Woodbury (1930), Knowlton and James (1932), Knowlton and Thomas (1936), and Knowlton, Maddock, and Wood (1946).

Studies on body temperature have been carried out by Lichten (1965). Mueller (1969) recorded the mean body temperature of graciosus from Yellowstone National Park. Other studies on thermo-regulation in species of Sce1oporus have been carried out by Cole (1943), Cowles and Bogert (1944), Bogert (1949), Larson (1961), and Brattstrom (1965).

Growth studies on S. g. graciosus at Yellowstone National Park were done by Mueller and Moore (1969); however, the results were based on few individuals. Stebbins (1944) studied the growth dynamics of California populations of S. g. gracilis. Tinkle (1973) has provided an extensive population analysis of the sagebrush swift in southern Utah.

There have been a number of ecological studies of other species of Sce1oporus. A study by Blair (1960) on S. olivaceus in Texas includes reproductive cycles, population dynamics, predation, and home range. Mayhew (1962, 1963a, and 1963b) studied the size of home range, reproductive cycles, and growth of S. occidentalis in California. Fitch (1940) studied the growth and behavior of S. occidentalis; Wilhoft and Quay (1961) reported its testicular histology and seasonal changes. Other studies on the western fence lizard have been made by Johnson (1965—food habits), Davis (1967-growth dynamics), and Tanner and Hopkin (1972)—production, growth, and home range. Crenshaw

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(1955) studied the reproductive cycle, habitat, and growth of *S. undulatus*; Carpenter (1959) studied population dynamics. Crisp (1964a and 1964b) examined the female and male reproductive cycles in *S. cyanogenus*. Zweifel (1949), Carpenter (1960), and Goldberg (1970a, 1970b, and 1971) studied ovoviviparity, parturition and behavior, and histology of the reproductive cycle, respectively, in *S. jarrovi*. Methodology and understanding of *S. g. gracilus* have been enhanced by these studies.

MATERIALS AND METHODS

Field work was started in the spring of 1970 on a study plot at the eastern edge of the Brigham Young University farm, southeast of Spanish Fork, Utah. The plot is 1.2 hectares set with rows of stakes at right angles, each stake being 12.2 m from other stakes. At the base of each stake a can trap was buried flush with the ground level as explained by Tanner and Hopkin (1972).

The elevation of the study plot lies between 1,493 and 1,554 m. The slope is approximately 40 degrees, facing west and containing a dry wash (Fig. 1 and 2A-B). The wash creates north- and south-facing slopes within the plot. The substratum on the south-facing slope was developed from a large talus slope which is light in color and of a fine gravelly nature. Small rocky outcrops and large solitary boulders occur on both slopes of the wash. The area south of the wash (north-facing slope and southern end of plot) has a more humus soil but is still rocky and has a surface covering of small gravel in some areas.

Two days of each week were devoted to checking traps and two to nosing and returning lizards to the place of capture. Each lizard

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Fig. 1. Outline of study plot with dominant vegetation and topography indicated. BYU Farm, Spanish Fork, Utah.
Fig. 2A-B. Study plot habitat features. A depicts the south-facing slope and B the north-facing slope.
was marked by toe chipping and its weight, size, sex, and external appearance were recorded, as well as body temperature at the time of capture. Air temperatures at approximately 3 mm and 1 m above the substratum were taken soon after noting the lizard's temperature. Notes on behavior, activity, and feeding were also recorded while working in the study area. A hydrothermograph was used to record weather data on the study plot, and United States climatological data were obtained from a station located 2.5 km north of the study area. A vegetation analysis of all plant species occurring on the plot was made in 1971, while flowering species were collected throughout the year.

Lizards were collected throughout Utah County and parts of Salt Lake and Wasatch counties. These lizards were autopsied in the laboratory to analyze reproductive stages, weight of gonads, stomach contents, and fat body weights; these data were compared with external measurements taken from study plot lizards. Observations of behavior in the laboratory were made by keeping lizards in two boxes partly filled with sand, rocks, and pieces of wood, creating a suitable habitat. Eggs laid in captivity were incubated in the laboratory at approximately 28 C.

Male testicular cycles and meiosis in female ovaries were analyzed by histological sections. Stomach contents were analyzed with a stereoscopic microscope, and arthropod volumes were measured by water displacement in a 10-cc graduated cylinder. All statistical tests of results were at the 5 percent level of confidence. The statistical tests used were chi-square, analysis of variance, and the paired t-test.

Description of the Study Area and General Observations of the Research

Habitat

Study plot vegetation included annual and perennial herbs, shrubs, and trees. The dominant plant association consisted of bigtooth maple, *Acer griseum*; Gambel oak, *Quercus gambelii*; and sagebrush, *Artemisia tridentata*. Distribution of the oak and maple is depicted in Fig. 1. Subdominants, abundant in some areas of the study plot, include snakeweed, *Gutierrezia sarothrae*; *Petrodoria pumila*; blue bunch wheatgrass, *Agropyron spicatum*; muttongrass, *Poa longiligula*; needle grass, *Stipa comata*; and junegrass, *Koeleria cristata*. Some perennial and annual herbs were balsam root, *Balsamorhiza sagittata*, and two species of brome grass, *Bromus* spp. The dominant and subdominant plant types grew in clusters, with ample open spaces (Fig. 2A-B). This type of spatial arrangement appears to be necessary for *S. g. gracilis* to occupy an area.

Collection sites throughout Utah County where lizards were taken usually had the same general environmental features as the study plot. Most had Gambel oak, bigtooth maple, and sagebrush as associated dominants. Some collection sites supported *Juniperus osteosperma* or sagebrush only. Elevation of collection sites ranged from 1,371 to 1,981 m. South-facing slopes usually provided the best sites for collecting, primarily because these habitats were more often chosen by *gracilis* (Fig. 2A-B).

Summers are hot, with few overcast days from mid-May to mid-September and with average daily maximum temperatures ranging from 30 to 37 C for July. There are approximately 180 or more frost-free days from April through September. However, irregular cold fronts may periodically reduce activity in March through the first of May and in late September and October. Precipitation and temperature on the study plot are summarized in Fig. 3. The average seasonal temperatures were similar during the years of this study and the precipitation averaged about 10 inches (25.4 cm) during the activity season, 1 inch (2.54 cm) per month. The least precipitation occurred in late June, July, and the first half of August. The precipitation total was lowest in 1972 and highest in 1970 (March through August).

Emergence

In 1970, 1971, and 1972 the first lizards emerged when average daily temperatures reached 10 to 13 C (Fig. 3). These early animals were juveniles of both sexes and adult males. The first adult male emerged 19 days before adult females in 1970 (22 March/10 April), nine days earlier in 1971 (21 March/29 March), and 21 days earlier in 1972 (5 March/25 March)—an average of 16.3 days between male and female emergence. Males were caught soon after emergence (indicated by the moist mud on the body).

Seasonal and Daily Lizard Temperatures

Mean preferred body temperature for study plot adults taken for the season, June to September, was 32.6 (19.0-38.8) C, juveniles 33.1 (21.0-38.4) C, and hatchlings 31.2 (26.0-35.4) C. Hatchlings did not tolerate temperatures much above 36 C. Temperature observations from the field for hatchlings during August and September ranged from 26.0 to 35.5 C. Periods of
20 to 30 minutes in a paper bag at temperatures near or above 38 C proved fatal, suggesting a lower critical thermal maximum for hatchlings than for adults.

Lizards emerged from overnight retreats with body temperatures of 16 to 21 C. Basking range was 21 to 28 C and normal activity range was 28 to 37 C. Adult and juvenile lizards were able to tolerate temperatures of 38 to 40 C. The critical thermal maximum in the laboratory was 43 C for an adult male and 44 C for an adult female. They were captured in March and April and kept in captivity at temperatures of 24 to 27 C.

In Fig. 4, the average temperatures of males and females are compared to temperatures of air 3 mm and 1 m above the substrate. During periods of intense heat in July and August, lizards could be found only in the oak-maple thickets and under sagebrush, rocks (crevices and overhangs), and other forms of cover. Some remained under cover until the heat of the day passed, while others in the oak-maple thickets were more active. The contrast between periods of low and high activity between 1000 and 1200 hours in July and August is represented in Fig. 5. Some lizards were at the basking areas before sun up during June, July, and August. This activity was seemingly caused by early morning light and high temperatures (15-17 C).

Daily and Seasonal Activity

A summary of the daily activity for study plot lizards during the 1971 activity season is diagrammed in Fig. 5. High temperatures for

Fig. 3. Precipitation (columns) and temperature (lines) by month for study plot for 1970 through 1972. Shaded columns represent 1970, vertical lines 1971, and horizontal lines 1972.
of several days, stopped all activity in the field. One or two days of warming were required before full activity resumed. Heavy thunderstorms during June, July, and August stopped activity periodically. Lizards reappeared as soon as the sky was clear. They basked for 10 to 20 minutes, or until body temperatures rose sufficiently. If a storm came late in the afternoon, they did not reappear until the next day. Cold fronts in September and October interrupted activity in much the same manner as earlier in the year.

**Slope Preference**

The number of lizards observed per hectare on each slope of the plot is summarized in Table 1. Adults and juveniles preferred the south-facing slope throughout the activity season. Hatchlings, after emergence, followed the same trend. Little activity occurred on the north- and west-facing slopes.

**Hibernation**

Hibernation of adults began in late August or early September and was recognized when individuals were no longer seen at their basking stations. Juveniles remained active until mid- or late September and hatchlings remained active until mid-October. One place of hibernation was found when an adult male was sighted on 10 March at the opening to a rodent burrow. He was completely covered with mud, indicating a recent emergence.

**Feeding Behavior**

On 28 April 1971 an adult female was observed climbing on sagebrush and feeding among the foliage. On 13 July 1971 an adult male ran a few feet from the cover of a small oak bush, grasped a large grasshopper. ate it, and then returned to the oak bush. The lizard shook the prey by lateral movements of the head before swallowing it. On 25 May 1971 an adult male was observed moving up the trunk of an oak tree and feeding on small insects. Though specimens ate both large and small prey while in captivity, they rubbed the sides of their heads on the substrate while eating the large prey.

**Aggressive Behavior**

Aggression in the field and captivity was observed in many forms in all age classes and in both sexes. An example of such aggression between territorial males follows. Chased into the territory of another by the observer, the intruder was immediately challenged by the resident and a melee of biting and rolling on-

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**Fig. 5.** Number and age of lizards observed, plotted against time of day, throughout the activity season of 1971 and March 1972. Solid line represents adults; dashed line, juveniles; dotted line, hatchlings.

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air at 1 m and 3 mm above the substrate in late June, July, and August ranged from 34 to 40 °C and from 43.2 to 45.0 °C. Temperatures above 50 °C for actual substrate surface were noted frequently during the afternoons of the warmer months. Our data indicate that adults and juveniles have the same daily activity throughout the year, with the activity of juveniles extending into September.

**Local Weather Conditions**

Periodic cold fronts in March, April, and early May, if severe enough and over a period...
sued, followed by a breakaway and standoff of about five centimeters. Bodies were compressed laterally to show the blue sides. Each stood high on all limbs with the back slightly arched and the dewlap lowered. Laboratory observations of territorial males revealed that the resident was always able to vanquish the intruder.

The following description covers all major actions observed in captive interactions. The intruder was placed in the box of the resident, whereupon he immediately stood high. The resident moved toward him from the side, moving his head to either side as he approached, as the intruder moved away sideways. Then the resident positioned himself parallel to the intruder, facing the opposite direction, and stood high on both limbs, compressing his sides to show the blue and lowering his dewlap. He then made a quick strike at the intruder, who ran, followed closely by the resident. When they stopped, the intruder assumed a position of passiveness with his head and tail lowered and with his body pressed low to the ground. The resident repeated the parallel body stance and then moved at the intruder, who again ran. This was repeated three times (Fig. 6A-B). Field observations in which a biting melee occurred often resulted in a temporary standoff until one was vanquished. Juvenile intruders were not tolerated by adult males and were immediately chased from the territory.

Females also reacted aggressively toward males after they had copulated. Such females, when approached by a male, flattened the body laterally, lowered the dewlap, pointed the tail upward and arched the body (Fig. 6C-D). Sometimes a female would move toward the male in a challenging posture and he would move away. Other times the female assumed this pose at the mere approach of the male and hopped on stiff legs toward him.

Table 1. Preference of adults, juveniles, and hatchlings for north-, south-, and west-facing slopes of the study plot. These values are ratios (number of observations) by month, which are based on the total number of observations on each slope divided by the area of each slope.

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Basking and Panting

All age classes were observed basking on the substrate, rocks, boulders, and branches of sagebrush, under bushes, and along the main branches of oak and maple trees. Basking usually began in the morning just after the rays of the sun had spread over the study plot. The lizard's ventral surface was in direct contact with the substrate. In captivity, basking behavior under sun lamps was essentially the same. On several occasions lizards were observed panting, opening the mouth and going through the motions of breathing rapidly. In captivity, panting occurred at room temperatures of 37 to 40 C; field observations were similar.

Pushups

Sceloporus gracilis was not included in the behavioral studies of Purdue and Carpenter (1972a and b). Because of the specialized nature of their study, we have not attempted to duplicate it for gracilis. Our data are general and provide only field observations. Pushups were observed in all age classes and in both sexes. They appear to be most important in courtship and territoriality behavior. Males often climbed on a rock or some other object and then engaged in one low pushup and stopped; this was sometimes followed by a second (high) and a third (low) one. Other pushup sequences are possible, but the above is the most normal and may be repeated several times. During the breeding season, males did pushups as they moved through their territories. When a female was encountered, he performed while slowly approaching her. At this time of the activity season, or while in the presence of females or other males, pushups were performed very high on the forelimbs. As he approached to about 7 to 10 cm from the female, the sequence was one low and one or two high pushups.
Fig. 6A-D. Aggressive behavior between males (A and B) and between females and males (C and D).
Fig. 6 A-D (Continued)
Reproductive Behavior

Mating behavior was observed eight times in the field and three times in captivity. On 4 June 1971 a female moved a distance of approximately two feet through a bush after being disturbed. It was then noticed that she carried a male with her. He had hold of her neck, was in a dominant position over her body, and was doing partial pushups while holding on to her. The posterior part of his body was then brought under the female, putting the vents into contact. The hemipenis was inserted into the cloaca as the vents came into contact. There was no movement of the posterior part of the male's body and the hemipenis was held inserted for approximately eight seconds, after which the female broke away, leaving the male stationary. He pursued her persistently for a few feet with the tail raised and the hemipenis still everted. It took approximately one minute for the hemipenis to be retracted. The male exhibited an erratic pursuit of the female in contrast to normal running and courting. As males approached females in the field, they did pushups and rapidly bobbed their heads. Females were grasped anywhere from midbody to just behind the ear, and males remained in a dominant position over the female for 8-10 seconds before attempting to copulate.

Captive reproductive behavior was similar, but with the following variations. When a male first noticed the female, he approached her with his head bobbing. The female was passive, not moving and remaining low to the ground. The male grasped the female twice before taking a firm grip on her shoulder, then assuming a dominant position over her. A few seconds elapsed without movement before copulation occurred. The hemipenis contracted rhythmically in waves of approximately two per second. After a short period of separation and reintroduction, the male no longer approached the female. The basic posture of the male and female during copulation is shown in Fig. 7A-C. One male rubbed the vent on the substrate after the hemipenis had been retracted. In a few instances the male did not perform pushups or head bobbing before he grasped the female. Actual times of copulation (contact of genital organs) in captivity ranged from 5 to 10 seconds. The tail of the female in each case thrashed during copulation.

A complete sequence of egg laying was not observed; however, laboratory observation revealed that females dig into the substrate 15 to 20 cm, lay eggs, and then fill in these holes as they return to the surface.

Food Habits

The contents of 393 stomachs were examined in 1971 and 1972. All age groups throughout the activity season for both years were included. Data in Table 2 indicate the major families of arthropods that were preyed upon by S. g. graciosus.

Data indicate a seasonal fluctuation of prey items taken by two age groups in 1971 at the ordinal level. In both years lizards were opportunistic in their feeding habits, with monthly changes in diet following the changes in abundance of different orders of arthropods. In each age group, in both years, the priority of numbers and consistency of orders eaten in each month were essentially the same.

The number and size of prey items consumed each month by adult males were noticeably different from those consumed by females. For example, of 1,383 Hymenoptera, 991 (predominantly ants) were consumed by females; of 284 Coleoptera, 149 were consumed by males. With regard to total numbers of all orders eaten by females, 1,494 of 2,157 were consumed, indicating that females consume a larger number of items than males. When considering volume, the order of priority for food items changed. For example, Hymenoptera were the most frequent stomach item; however, in adults they made up 5.47 cc, while Coleoptera made up 7.26 cc. Total volume was 14.80 cc for males and 15.70 cc for females. These volumes indicate that, while females eat more, they eat smaller prey; total volume consumed is not significantly different.

Ontogenetic Changes in Color and Color Pattern

According to Stebbins (1966), hatchlings (24-27 mm SVL) have the characteristic color pattern of adults. In the central Utah population we find that males at 24.5 to 32.0 mm SVL begin to show faint blue green ventral belly patches. By the time they average 34 mm SVL in mid-September, the ventral patches are edged with black. The blue is still blended with the green and is not yet as dark as in adults. Males reaching 36 to 39 mm SVL show traces of throat baring. Females may show a faint outline of ventral patches between 32 and 35 mm SVL.

Juvenile males continue to develop darker blue patches ventrally, and by late April and May (at approximately 40-45 mm SVL), they have essentially the same color pattern as adult males of 55 to 60 mm SVL. Juvenile males that are over 47 mm SVL in mid-May are essentially of the same brilliance as adults.
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Fig. 7A-C. Copulation sequence of lizards in captivity indicating major posture of the male and female.
Juvenile females lose the outline of a ventral pattern as they grow and do not become orange laterally until they become breeding adults.

When adult females emerge (March or April), there is no nuptial color laterally. The venter is white and the normal dorsal and lateral color pattern is present (Stebbins, 1966). In April and May, while the female cycle is undergoing vitellogenesis and the ovarian eggs are approaching ovulation (6.5-7.0 mm diameter), they begin to take on the orange coloration laterally. This color may extend from the head to the groin region and even onto the tail. Females reached their most brilliant nuptial colors while carrying oviducal eggs, between 27 August 1970 and 20 August 1971 which were very orange, but palpation revealed no oviducal eggs.

Adult males emerging in March have the characteristic color and pattern described by Stebbins (1966). The most brilliant period for the lateroventral blue and black is April through July, though some males may still be brilliantly colored in August. There is also considerable blue green in the lateral scales of the shoulder region and posteriorly onto the base of the tail. There is no blue green on the tail where regeneration has occurred.

Parasitism and Predation

Stomachs were removed approximately 3 to 5 mm below the pyloric sphincter. While removing stomachs from 690 specimens, one tapeworm was found in an adult male and one in an adult female. These were identified as Oochoristica scelopori; no nematodes were found. External parasites were either ticks or mites (Acarina) and were found on specimens from West Canyon, Utah County.

Examination of 690 preserved specimens from Utah County and parts of Wasatch and Salt Lake counties, revealed only two cases where the cardium of the lizard was discolored and a heavy growth had replaced the thin transparent structure. Abnormalities were not ob-
served internally on autopsied specimens. Animals from the study plot were checked externally only and no infections other than an occasional swollen toe from identification clipping or natural loss were observed. Infection or swelling at the point of tail breakage was not observed.

Predation was not witnessed in the field. Utah County records indicate the night snake *Hypsiglena torquata* as a predator. Possible predators in sympatric areas may include predaceous reptiles, hawks, and mammals.

**Ontogenetic Changes in the Tail**

Ten arbitrary size classes were chosen and the mean SVL and tail length were taken on 20 animals in each size class except for the smallest and largest sizes. The mean SVL of each size class was plotted against the mean tail length (Fig. 8), contrasting males and females throughout their growth from hatchlings to adults.

**Tail Breakage of Study Plot Lizards**

Hatchlings, juveniles, first-year (after second hibernation), and older adults were analyzed in 1970 and 1971 for tail breakage. Males and females were contrasted throughout the activity season. These data can be summarized as follows:

- **Adults**: males 14 of 69 (21 percent), females 18 of 116 (15 percent); juveniles, males, 10 of 97 (10.3 percent), females 8 of 131 (6.1 percent); hatchlings, males, 5 of 247 (2 percent), females 10 of 231 (4.3 percent). There was an increase in breakage from hatchlings to adults (3 percent, 8 percent, 18 percent). One specimen from the field and one from the study plot had bifurcated tails.

- **The regenered portion did not have the same color or color pattern as an intact tail. This was strikingly apparent in males with the blue green on some lateral scales which extended onto the proximal half of the tail.**

**Average Size of Females at Sexual Maturity**

Sexual maturity in females was determined by noting the development of the gonads. The main criteria used were the presence of yolking follicles in the ovaries, ovudal eggs, or corpora lutea during the reproductive period. Most reproductive activity took place before 1 July; therefore, 1 July was used as the date females were considered mature for that particular year. All females 33 mm SVL or larger were considered mature. Study plot females found with eggs (based on palpation and color and weight of females) were in this range. Three females which were 47, 48, and 49 mm SVL, autopsied on 28 May 1970 and 7 June 1971, had small yolking ovarian eggs 2 or 3 mm in diameter. Egg development in these females was late in the season compared to other larger females. If these eggs were eventually laid, it would have been late compared to the average time taken to reach ovulatory size and egg laying. Such individuals made up only 1 percent of the breeding population.

**Follicle Growth**

As females grew from hatchlings to adults, the average number of unfollicled follicles increased in number and enlarged. Ovaries were visible as small white tissue masses in the smallest hatchlings captured (25 mm SVL). The August hatchlings between 25 and 33 mm SVL may have none; however, 70 percent had one to four follicles (Table 4). September and October hatchlings, just prior to hibernation, showed an increase in size and number of follicles. During hibernation there appeared to be little growth in the ovaries, although we did not examine hibernating lizards. In the spring, follicles continued to increase in size and number until June, then decreased in July and increased again in August (Table 3).

Adult females underwent seasonal changes

**TABLE 3.** Number of unfollicled follicles in hatchlings and juveniles by month, 1970-71. All measurements are

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<th>HATCHLINGS</th>
<th>March-April</th>
<th>May</th>
<th>June</th>
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</thead>
<tbody>
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<td>Mean</td>
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<td>40</td>
<td>11.3</td>
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<tr>
<td>Range</td>
<td>30-37</td>
<td>1-1.1</td>
<td>7-13</td>
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<td>Number*</td>
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</table>

*Number of specimens examined.
Fig. 8. Mean snout-vent length of sagebrush swifts plotted against mean tail length (mm) for 1970-71. Females are represented by solid line and males by dotted line.

in the number and size of unyolked follicles (Fig. 9). The total number of follicles may change seasonally, with the lowest number occurring in July after the eggs are laid (Table 4). Our data indicate that from March to June a decrease in size and number of unyolked follicles above 1.5 mm occurred. Between 1 July and 15 August only five follicles above 1.5 mm were seen in 1971 and only one in 1970 (Fig. 9). This indicates that follicles show a reduction in size in July and the first half of August. From mid-August until hibernation there was an increase in mean follicle number and size. In September follicles ranged between 1.9 and 2.0 mm, appeared to be yellowing, and perhaps were beginning vitellogenesis.

In Fig. 10 the total number of follicles in each of five lizard size classes are compared, indicating that unyolked follicles increased in number as females became larger and older.

**Meiosis**

Serial histological sections revealed that follicles went through meiosis both in the fall (August-September) and spring (March-April). Eleven of the first 12 females collected from 29 March to 29 April 1971 were undergoing meiosis. Of the last 13 females captured 24 August to 23 September, 12 were undergoing meiosis. The size range (determined from slides) of follicles undergoing meiosis was 0.5 to 1.5 mm—average size in the fall being 0.96 and in the spring being 1.05.

**Yolk Deposition**

Females were not yolking follicles in August. In September follicles were slightly larger and from cream to light yellowish in color. All began soon after emergence in the spring. Yolking eggs continued to increase in size up to the

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**TABLE 4. Fluctuation in the number of unyolked follicles in the ovaries of adult females, 1970-71.**

**HATCHLINGS**

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**JUVENILES**

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time of ovulation. The smallest diameter for definite yolk deposition (by color) ranged from 1.5 to 2.0 mm (late March and early April), which is close to the approximate size of meiotic follicles (mean 1.30 mm). Yolking eggs increased from an average of 1.75 mm in late March to a peak of 7.09 mm in diameter in the first half of June, with a range of 6.5 to 8.5 mm just prior to ovulation. This was an increase of approximately .07 mm per day. Weight followed the same trend as size. Eggs less than 2.0 mm in diameter weighed less than 0.1 g. In June oviducal eggs averaged .21 g per egg (N-65) with a range of .14 to .28 g per egg. These were from clutches ranging from two to seven eggs. Yolk deposition occurred in the populations from 29 March to 3 July, a period of 97 days.

**Ovulation**

Eggs passed into the coelom and from there into the oviducts. Ova in the coelom were flaccid and the only structure holding the yolk was the vitelline membrane. One female (BYU 3338, 64 mm SVL) found on 10 June 1971 contained some eggs recently ovulated, two in the coelom, and others entering the oviducts—a total of seven eggs in the clutch. Judging from the delicate nature of ovulated eggs, it would seem that females might reduce their activity to prevent breakage; breakage was not observed. A female captured on 20 May 1970 had six eggs (three per ovary) and all were between 6 and 7 mm in diameter. In addition, there were two eggs (5 mm each) free in the coelom. They were greyish and slightly crenated in appearance, yet pliable and with discolored yolk. Ovulation in gracilis took place approximately between 2 June and 3 July 1971, the 32-day period between the first and last oviducal eggs. The majority of females were undergoing ovulation from 2 June to 24 June (22 days), at which time oviducal eggs and the first corpora lutea appeared. In 1970 the development of eggs was approximately 15 days later than in 1971. The actual time required for each stage (yolk deposition, etc.) remained fairly constant in terms of active days.

**Mating Time in the Field**

Copulations were observed in the field between 21 May and 4 June 1971 and in captivity between 2 June and 9 June. At this time males and females were seen together in the field in contrast to the periods before and after the majority of copulations. Observations of field and captive individuals from 21 May to 9 June suggest that the majority copulate over a period of approximately 20 days. This time period may extend earlier into May but probably not later into June, except in years with unusually late springs.
Egg and Clutch Size and Weights Following Oviposition

Clutch size and SVL for females laying eggs in captivity are listed in Table 5. Twelve clutches (68 eggs) were weighed and measured within one to five days after oviposition. The mean size of recently oviposited eggs was 13.4 x 7.9 mm with a range of 12.0 x 6.5 to 15.5 x 9.0 mm. The mean weight was .48 g per egg with a range of .30 to .76 g per egg. Compared to the weights of oviducal eggs, these recently laid eggs averaged .20 g more. They were also larger in size, 13.4 x 7.9 mm as compared to 12.0 x 7.1 mm. A few clutches were in moist sand for a few days and undoubtedly increased in size and weight by water absorption.

Size and Weight Changes in Gravid and Nongravid Females

The size and weight changes in females before and after laying and the time that elapsed between the periods are listed in Table 6. Compared to the average weight of clutches, the average weight per egg was .48 g (Table 5). These data also indicate that females that have laid eggs with an intervening period of 10 days or less show no difference in size (SVL) but weigh 1.5 to 3.0 g less.

Clutch Size, Clutches per Year, and Comparisons of Left and Right Ovaries and Oviducts

Clutch size in graciosus was determined after the method used by Tinkle (1961). The number of ovarian eggs, oviducal eggs, and corpora lutea in both ovaries and oviducts are listed in Table 7. Clutch size was 6.03 eggs per female. There were slight but not significant differences in the number of ovarian eggs, oviducal eggs, and corpora lutea. The mean for either left or right side was 3.00 eggs each. The overall mean clutch size for each of the three methods mentioned above was 6.22, 5.85, and 5.90 eggs per female, respectively.

Corpora Lutea

Corpora lutea of BYU 3338, which had just ovulated, were used as a standard of appearance; they were red (vascular), and the tissue proper was thin and translucent in appearance. Recent corpora lutea were large (3-4 mm in diameter) and doughnut shaped, with an indented area on one side near the center. They regressed in size by one-third (2-3 mm) and became less vascular and greyish in appearance, while the eggs remained in the oviducts. Soon after the eggs were oviposited, the corpora lutea turned yellowish, beginning a rapid re-

<table>
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<th>TABLE 5. Number and weight of ova 1 to 3 days after laying (1972) for 12 clutches laid in the laboratory.</th>
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<th>TABLE 6. Size and weight differentials of female lizards before and after eggs are laid (1970-71).</th>
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<tr>
<td>Average</td>
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* Captive.
Regression until they disappeared in approximately 10 to 12 days. Corpora lutea were found in the population from 2 June to 17 July 1970, a period of 45 days, and 15 June to 25 July 1971, a period of 40 days.

Atretic Follicles

Atretic follicles were of three types. First, yolking follicles were considered to be atretic if there were corpora lutea or oviducal eggs present. These follicles appeared to be the beginning of a second clutch; however, based on average time for vitellogenesis and oviducal development, they were late in the season for successful incubation. In addition, females were not found with oviducal eggs after the third week in July. Nuptial colors persisted beyond this date in only three individuals, but no eggs were found. Second, follicles that were few in number and appeared yolked in an ovary but were turning reddish yellow were considered atretic. These were apparently regressing in size. This condition was also observed before ovulation in a few females in which some yolked ova changed color and remained smaller in size. The third condition was that of crenulated ova in the ceolom. In all three types a total of about 13 percent of the females examined had atretic follicles.

Oviducal Egg Period in Oviducts,
Size and Weight

In 1971 oviducal eggs were found from 2 June to 10 July, a period of 38 days. Two captive females copulated on 7 and 9 June and laid eggs on 28 June and 2 July. These were periods of 22, 24, and 27 days, an average of 24.3 days, which is the approximate time eggs are in the oviducts, assuming that ovulation occurs at or just after copulation. Both 1970 and 1971 oviducal eggs were used for calculating size and weight of eggs. Oviducal eggs were weighed with the oviduct, which added a slight bias to the weight of the eggs. They averaged 12.0 x 7.1 mm with a range of 10 x 7.5, 11 x 6.5 mm to 14 x 8, and 15 x 7 mm. The average weight per oviducal clutch was .28 g with a range of .20 to .38 g. This was .07 g greater than ovarian eggs. In 1971 oviducts were vascularized from 10 May to 10 July. After oviposition the oviducts are no longer convoluted and lose their vascularization.

Ovumigration and Oviduct Anatomy

Transceolomic migration occurs frequently in gracilis. Of 48 females having oviducal eggs, 20 had eggs in the right or left oviducts that were of a different number than corpora lutea in the ovaries. Forty-two percent of these females had undergone transceolomic migration of ova. Therefore, ovumigration at the time of ovulation is essentially a 50:50 relationship in which any ovum has an equal chance of entering either oviduct. This has a limitation apparently in that no more than five eggs were ever found in one oviduct. The trend of migration follows several patterns. First, there is an even number of corpora lutea in the ovaries with a reduced number in one of the oviducts. Second, they are exactly reversed from ovary to oviduct—e.g., two corpora lutea in the right ovary, but three eggs in the right oviduct. Third, corpora lutea are of unequal numbers in the ovaries and there is a highly unequal number of eggs in the oviducts. For example, BYU 32616's right oviduct had three eggs and the right ovary had one corpora lutea. The fourth condition is an equal number of corpora lutea in the ovaries with an equal migration of ova to each oviduct.

The oviducts approaching ovulation appear convoluted and vascularized. At their anterior end they open into a slitlike ostium. The ovaries are attached dorsally to the body wall anterior to the oviduct. The oviduct is laterally displaced in relation to the ovary, with the expanded ostium lateral to the adjacent ovary and also at an angle to it.

Oviposition

Egg laying occurs after eggs in the oviducts have received the membranous shell. The period during which females are laying eggs, oviposition, was calculated from study plot and collection data (1970-71). At our study plot the egg-laying period lasted 29 days. (3 July-31 July) in 1970 and 31 days (19 June-20 July) in 1971. Clutch size increased as females grew in size (Fig. 11).
Incubation Period

The period from the first captured female with only corpora lutea to the first hatchling extended from 3 July to 24 August 1970, 21 June to 6 August 1971, and 17 June to 10 August 1972, periods of 43, 48, and 55 days, respectively. The incubation periods from field data were as follows: 1970, 6 July to 17 August; 1971, 19 June to 1 August; 1972, 1 July to 10 August (periods of 43, 44, and 41 days, respectively, for a combined average of 43 days). The incubation period for eggs from the time of oviposition in 1970, combining the field and study plot data, was 48 days. In 1971 the period was 46 days, and in 1972, 48 days. The average period combined for three years was 47 days. The data also indicate that the incubation period of 1970 was approximately 15 days later than for 1971, with 1972 in between. In addition to this indirect data, nine clutches of eggs were incubated in the laboratory at 27 to 28 °C in quart jars partly filled with moist sand. The overall average for these clutches was 49 days, a figure similar to the field and study plot data. The average period for clutches where the exact date of laying was known was 46 days, which closely approached the overall average. From these data was derived the average incubation period from the time the eggs were laid: 48 days, with a range of 44 to 52 days.

Oviducal eggs taken from field females and those captive females having recently oviposited each showed a distinct area where the embryo had probably been growing since the time of fertilization. Known measurements of captive females placed the eggs in the oviducts for a period of approximately 22 to 27 days. This was particularly true if eggs were ovulated shortly after copulation (1-5 days) and if they were fertilized at or about the time they entered the oviduct. Data concerning ovulation time and copulation period strongly suggest that fertilization occurred at or shortly after the eggs entered the oviducts. If this were the case, it would add approximately 25 days to the actual incubation period.

Sixty-eight eggs were laid and recovered from the pen where 13 females were kept. Eight eggs (11.7 percent) were infertile. Seven clutches did not contain infertile eggs, two had two each, and four had one each. Infertile eggs appeared softer and amber in color. They did not attain turgidity, were soon attacked by fungus, and, unless removed, began to contaminate the entire clutch. From the remaining 60 eggs, 11 died just before their clutch mates hatched. The embryos were between 20 and 23 mm SVL. The yolk sac was intact with a small amount of yolk still remaining. The 49 eggs remaining were reduced by fungus contamination and other causes, leaving only 34 eggs that hatched.

Average Size of Males at Sexual Maturity

Sexual maturity was determined by gonadal development, size, and glandular development. The main criterion used was the presence of spermatozoa in the testes and epididymis during the reproductive period. As in females, 1 July was used as a seasonal date when males, on the basis of size, were considered mature. Some juveniles may reach mature size by the second week in July and may be mistaken for adults even though they are not sexually mature. Based on the above criteria, males 52 mm SVL were considered sexually mature. There were three exceptions (1 percent of total mature males) in 1970 and 1971 field specimens. These three were 43, 46, and 50 mm SVL. In 1970 and 1971, none of the breeding population of plot males were below 52 mm SVL. This was based on external appearance of males (ventral color, discolored pre-anal area, and swollen tail base). While a few juvenile males in 1972 appeared as above in late June and early July, our autopsy data indicate that juveniles are not functional until after the second hibernation.
**Spermatogenic Cycle**

Histology of the testicular cycle in males was grouped into eight stages by Mayhew (1971). Stages of mature males during the 1971 activity season are listed in Table 8. This table and Fig. 12 to 14 depict mean seminiferous tubule diameter, gonad weight, and epididymis epithelial height (thickness) by month and are used in constructing the spermatogenic cycle of 1970 and 1971 in the following sections.

In March 1970 male gonads were at stages 3 and 4. Seminiferous tubule diameter averaged...
209.6 um (range 185-225 um). Epididymis epithelium was in a pseudostratified condition, with a height of 18.2 um (range 15-21 um). Both testes averaged .21 g per lizard in March, with a range of .13 to .35 g. Adults in April ranged from stages 3 to 6 and seminiferous tubules had reached their maximum diameter (mean = 221.0 um, range 196-260 um). Epididymis epithelium was proliferating and had an average height of 24.7 um (range 10-31 um). Gonad weight in April averaged .25 g per lizard, with a range of .14 to .34 g.

Adult males in May were at stages 6 and 7. The average diameter of seminiferous tubules was 206.4 um (range 164-225 um). The first males with spermatozoa in the epididymis were collected on 29 May 1970. Epididymis epithelium height averaged 34.6 um (range 32-35 um). Gonad weights reached their peak in May, averaging .30 g per lizard (range .23-.37 g).

In June males were still at stages 6 and 7, with the predominance at stage 7. All had spermatozoa in the epididymis and were capable of inseminating females. Seminiferous tubule diameter was 157.7 um (range 145-203 um). Epididymis height averaged 34.0 um, with a range of 26 to 45 um. Gonads averaged .14 g per lizard (range .09-.18 g).

In July males were predominantly at stage 8, with only one at stage 7. Seminiferous tubules reached their lowest level at 73.8 um, with a range of 54 to 90 um. The epididymis contained spermatozoa until 11 July. Epididymis height for July averaged 22.5 um (range 17-32 um) and began to decline on or before 11 July. Gonad weights in July reached their lowest level with a mean of .01 g per lizard (range less than .01-.02 g).

In August and September males reached stages 8 or 1, with the majority at stage 1 (26 out of 31). July and August were seemingly the end of one reproductive cycle and the beginning of the next. Diameter of seminiferous tubules for August and September averaged 107.2 and 175.6 um, with a range of 71 to 154 and 138 to 195 um, respectively. The epididymis height was at its lowest level with an August average of 15.8 um (range 10-21 um). September epididymis height was uncertain because of insufficient sample size. Only one specimen had an epididymis of 10.0 um. Gonads averaged .04 and .15 g per lizard for August and September, with ranges of .01 to .17 and .07 to .19 g, respectively.

In 1971 males emerged in March, at which time the gonads were in stages 1 to 3. Seminiferous tubule diameter averaged 186.2 um (range 164-210 um). Epididymis epithelium was pseudostratified, with an average height of 16.1 um (range 10-20). In March gonad weight was .21 g per lizard, with a range of .11 to .26 g.

Males in April, May, and June followed essentially the same sequence in development as in 1970. There were more discrepancies in July, however. Individuals were observed to be in stages 7, 8, and 1. By late August and September males in 1971 were predominantly at stage 1, with only two at stage 8. The seminiferous tubule diameter began to increase and averaged 110.0 and 165.7 um (ranges of 50-144 and 138-195 um). Epididymides were pseudostratified and their heights were 18.7 and 9.0 um (ranges 10-27 and 10-18 um). The weights of gonads were beginning to increase, with averages of .04 and .15 g per lizard, with ranges of .10 to .12 and .04 to .22 g.

The spermatogenic cycle in 1970 was approximately fifteen days later than in 1971. In March 1970 lizards were at stages 3 and 4, while 1971 lizards were at stages 1 to 3. It appears that males in 1970 were more advanced than those in 1971 even though in both years they emerged at approximately the same time. However, by the first half of May 1971, lizards were more advanced than those in 1970. By April 1971 epididymis epithelium had proliferated almost to its maximum for the year, whereas 1970 epididymides were considerably lower in epithelial height (Fig. 12). In addition, epididymides in 1970 were not found with spermatozoa until 29 May. However, to be comparable to 1971 this should have occurred on approximately 15 May. In contrast to the date of 15 May for 1970, 1971 lizards contained spermatozoa in the epididymides ten days earlier on 6 May.

**General Trends**

Even though adult and juvenile males enter hibernation with gonads approaching maximum size, they continue to increase during hibernation and develop more rapidly after they emerge. Peak development of gonads is in the latter half of April and the first of May. Male epididymides usually contain spermatozoa in late May and are capable of insemination. Spermatozoa remain in the epididymides until mid-July. By the latter part of June, the epididymis epithelium is sloughing and the lumen is full of cellular debris. Thus, active spermatozoa are in the epididymides from 1.5 to 2 months each year, a period much longer than that normally used for copulation (as based on field observations over three seasons). By the end of May the gonads are regressing. They continue to regress through June, and by mid-July are at their smallest size
Bingham males decline a percent Sept. females be Adults are the was both is the ion glandular This June older Aug. moist 1970 fat females—bodies white May gland increase or In 1971, faint 1970-71 the give simulate the July rows size.<br><br>Fig. 15. Summary of various reproductive stages of adult S. g. graciosa. Both 1970 and 1971 data are combined in order to simulate the average yearly trend.

(Fig. 12-14 and Table 8). In August the gonads again begin to increase in the size of seminiferous tubules and weight, continuing until the lizards hibernate in late August and early September.

Male stages are compared with those of females in Fig. 15. The combined time periods (1970-71) are used to give the general yearly trends of male lizards in relation to females. Our data for reproductive cycles in this species are generally similar to that reported by Woodbury and Woodbury (1945).

**Pre-anal Gland**

After considerable handling of lizards to obtain field measurements, it was noticed that males left a moist area on the transparent ruler. This moist area was directly in front of the vent and was discolored in relation to other areas anterior to it on the abdomen. At first the moistness was suspected to be from the normal cloacal discharges; however, careful checking determined it to be a glandular secretion which darkened the scales in the pre-anal area of adult males during the copulatory period. Histological sections of adult males show that there is indeed a gland just anterior to the cloaca, under the epithelial tissue—a duct gland, with cells lining a lumen. The details are presented in a separate report (Burkholder and Tanner, 1974).

**Color in Males**

Adult males are most brilliantly colored from April until mid- or late July. During this time, the ventral and ventrolateral portions of the head, neck, lateral and ventral chest, abdomen, and the lateral part of the tail are colored. These colors differ from the white ventral base color and brown dorsal ground color. The range of color varies from black to light orange. During the height of color display, an average male has barring of black and light blue interspersed with white on the throat scales. The chest has black areas (irregular) on a white base. The ventral patches begin behind the axilla and extend to the groin, with the inner edge lined with one or two rows of black scales. Proceeding from the black edge, the scales are deep blue and gradually lighten from the ventral to the lateral, becoming greenish yellow in the region of the light lateral body bar. The patches are separated by 3 or 4 rows of white scales. Laterally, starting in the axilla, the scales of the light lateral bar exhibit some orange, but it is faint and—in contrast to females—usually does not extend to the groin region.

**Fat Body Relationships in Adults**

In the sections on ovarian cycles and spermatogenesis, considerable emphasis was placed on time difference between the cycles. In the analysis of fat bodies, the data for 1970 and 1971 are combined to increase the number of samples and demonstrate the difference between male and female cycles. Differences between the two years are discussed briefly, but the bulk of this section will deal with male and female differences in all ages. All figures are based on mean fat body weight divided by mean body weight, giving a percent of body weight for the fat body.

In 1970 fat bodies in males were smallest in June; 1971 males had already started their increase (by weight) prior to July. This difference is significant because in both years fat bodies began to decline in size and weight by late April. In 1971, lizards completed their gonad peak (by weight and size) in the first half of May. In 1970 males reached their gonad peak in the latter half of May and did not begin fat body buildup until June (Fig. 16).

Comparisons of females for these years indicate the same time lag as males in fat body decline and buildup, although the decline in
1971 was considerably faster than in 1970. Fat bodies in 1971 were at about the same level in April as those of 1970 were in May (.2 percent difference). In May 1971 they were near their smallest size-weight (.1 percent weight), but in 1970 fat bodies were almost the same weight as in 1971. By June both were at their lowest weight and began an almost identical increase from that period to hibernation.

In Fig. 17 the mean body weights by month and the percent of body weight for fat bodies are compared. It is apparent that females had larger fat bodies than males except in June and July. The June discrepancy is explained by noting that females were at their lowest fat body average and their highest average body weight (1.08 g greater than males). If the average weight of oviducal eggs is subtracted from body weight, the percent of body weight for fat bodies will also be higher in June for females. With few exceptions, all sexual activity is over by July, and female mean body weight is almost the same as that of males. This similarity in body weight in July makes it apparent that females have larger fat bodies than males in August and September (1.9-1.2 percent, respectively).

**Juvenile Gonad and Fat Body Relationships**

Juvenile fat body fluctuations are depicted in Fig. 18, along with average weight per month. These data indicate that juvenile males follow a fat body and gonad cycle similar to that of adult males, which is most apparent from July to hibernation. In addition, hatchlings also show a buildup of fat bodies before hibernation.

**Hatching Home Range**

Hatchlings actually do not have a home range; therefore, the term area of activity is proposed. They reside in their areas of activity after hatching and are slowly dispersed before hibernation. Retrapping data suggest that some
moved considerable distance from the place of their first capture, whereas others were captured many times in the same general area. The areas of activity for male and female hatchlings are .0114 and .0110 ha.

There is a definite tendency for hatchlings to set up a small area of activity. We observed a male hatchling exclude a female hatchling from a particular bush he occupied. Two representative hatchling areas of activity are diagrammed in Fig. 19.

**Juvenile Home Range**

Juveniles were often observed being chased from the established residence of adult males. The recapture data indicate some juveniles establish a home range in the same area they used as hatchlings. Five records of juvenile movement from their initial capture as juveniles to a new home range (periphery of new home range) averaged 75.6 m, with a range of 56.0 to 92.6 m. This indicates that many, if not all, juveniles had established new home ranges during June and July.

Female 1-6-9 traveled 77.7 m from her initial capture on 27 May to a home range in which she remained from 20 July until 6 August of the same year. She was captured four times and on 31 August was found 12.5 m from the capture point of 27 May (a return distance of 62.8 m). In addition, she was found in this same home range as an adult the following year. This movement was from the south-facing slope through the wash across the north-facing slope to the west-facing area and then back. A male (1-4-10) lived in a specific area as a hatchling in October and during the following year from 12 June to 27 July. On 13 August he was found 67.0 m north of his previous home range and on 17 August was 65.5 m east of the 13 August capture, a total of 95.1 m (straight line) from the center of the original home range.

Juvenile home ranges averaged 2.8 times larger than the area of activity of hatchlings. The areas were essentially the same for males and females (.0314 and .0316). Two typical home ranges are diagrammed in Fig. 19.

**Adults**

As adults, the first differences in the size of the home range between the sexes became apparent (.0423 and .0563). Male home range size averaged 24.9 percent larger than that of females. There was an overlap in the size, with the ranges for males 76.1 to 1521.5 and for females 71.4 to 887.6 sq m.

Home ranges of adult females and males averaged 25.0 and 44.2 percent larger than those of juveniles, though there was some overlap in size between their home ranges. The home range of two adults is shown in Fig. 19.

It appears that some adult home ranges may increase slightly in size, but the majority remain generally the same size and in the same area. A male (5-6) remained in his 1970 range at least until 28 May 1971. In 1972 he was captured 102.4 m southeast of his former range. Extended forays by males do not seem to be common. During the spring and early summer males are involved in courtship and in the defense of their territories.

Adult females appear to be restricted to home ranges except for extended forays to lay eggs. We have four such records, but the percentage of those leaving to lay eggs is not known. Adults show an overlap in home ranges, as do juveniles and hatchlings. The majority were located on the south-facing slope.

**Age Classes**

Three age groups are used in this study. The first group, hatchlings, appears in the population from about the last week of July through the first three weeks of August and remains active until hibernation in October. Upon emer-
gence from their first hibernation in March, they are reared as juveniles. Lizards remain juveniles during one entire activity season, although by August or September they attain minimum adult size. Lizards emerging from their second hibernation are adults. This group may be divided into first-, second-, and third-year reproductive classes. Our data do not go beyond the third reproductive year.

**Hatchlings**

In 1970 the first hatchlings did not appear on the study plot until 17 August. The 1971 and 1972 hatchlings appeared on 1 August and 10 August, respectively. In 1972, 13 adult females, kept in captivity, laid 68 eggs, of which 34 hatched. Measurements (SVL and total length) and weights were taken prior to 24 h after hatching and after five to seven days. The different measurements before and after the five to seven day period were .56 mm SVL increase, .92 mm increase in total length, and .107 g weight loss per lizard. For detailed data see Burkholder (1973). Using a paired t-test of difference, all means were significant at the 95 percent level. This indicates that the yolk present in the gut after hatching keeps hatchlings alive up to a week or more and may allow for some growth. Thirty hatchlings were measured, and only one was smaller (SVL) when measured after five days. However, in all hatchlings the weight decreased. The normal metabolism of the lizard would provide for some growth, the amount depending on the amount of yolk available. The average increase in size for six days was .050 mm SVL per day. It is seemingly very important that hatchlings have yolk in the midgut after hatching to sustain them until they can capture prey. Two hatchlings approximately three hours old were able to recognize prey and strike at it but were only able to handle small, soft-bodied insects (a 12-mm lacewing and a 5-mm leafhopper). It was only after six or seven trials that they could grasp the prey and swallow it. Although they had an instinctive ability to recognize prey and attack it, several days were necessary before they became successful in feeding. Recently hatched lizards in the field usually had empty stomachs.

**Size at Hatching and Growth**

Based on laboratory hatchlings, males and females averaged 24.81 mm SVL (N=19) and 25.27 mm SVL (N=13), respectively. Mean weight was .53 g for males and .56 g for females. Total length averaged 56.21 mm for males and 57.58 mm for females.

Once hatchlings were foraging, growth pro-

ceeded at a continuous rate. The average rate of growth in SVL and grams per day for 1971 and 1972 activity seasons are summarized as follows: males, .0841 mm and .0086 g; and females, .0841 mm and .0070 g.

These figures depict the average growth rate for all lizards (pooled N = 99 and 162 for males 1970 and 1971 and N = 113 and 175 for females in 1970 and 1971) in each year for the study plot population. A starting point for weight and SVL was taken from the average size and weight at hatching. The range was .513 to .857 mm, with an average of .0841 mm per day, which approximated the 30 laboratory hatchlings (.0800 mm per day without additional food). Weight increase was slightly different, with males showing a higher average than females (.00565 g to .00700 g per day). Considering the extreme fluctuations in weight, size in mm (SVL) may be a better indicator of growth. From these data it is apparent that males and females grow at essentially the same rate from the time of hatching until hibernation in October (Burkholder, 1973). In October 1970 males averaged 30.1 mm SVL and 1.09 g and females 30.2 mm SVL and 1.02 g. In 1971 both males and females averaged 32.3 mm SVL; however, males weighed more (1.28-1.13 g). Hatchlings in 1971 reached a larger average size than in 1970 (Fig. 20) because of a longer growing period brought about by an earlier oviposition. Individual growth rates for 20 hatchlings in 1970 and for 30 in 1971 are listed by Burkholder (1973).

The percentage of increase from hatching to hibernation in 1970 (65-day period) was 20.64 in SVL and 48.57 in weight; in 1971 (86-day period) it was 22.60 in SVL and 55.00 in weight.

**Juveniles**

The period of greatest growth is during the year after emergence from the first hibernation. Juveniles usually attain adult size by August, depending on the environment, and level off in September (Fig. 20-22). Study plot populations entered their first hibernation at an average SVL of 33.0, 31.6, and 33.1 mm for 1969 through 1971. Differences between hatchlings before hibernation (maximum size N = 40 and 45 for 1970 and 1971) and juveniles in 1971 and 1972 (March) were .95 and 2.06 mm SVL. Data indicate that little, if any, growth occurs during hibernation. This assumption is based on the similarity of the average size of the latest hatchlings seen in 1970 and 1971 and the earliest juveniles of the following years and is supported by losses in fat body weight (Fig. 18). Since fat stored in the tissues and fat bodies is the only source of energy during hibernation (approxi-
mately six months of cold and snow) it is unlikely that such storage is large enough to provide energy for growth. Temperature is also a limiting factor, since lizards are just below the frost line and metabolism is thus at a low level.

Each year (1970-1972) juveniles reached adult size at different times (Fig. 20). Some were adult size in early August of 1970 as compared to late July of 1971. Individual growth rates per day for 11 juveniles in 1970 are listed in Table 9.

The average rate of growth in mm (SVL) and g per day in 1970 and 1971 for males was .1230 and .1489 mm and .0200 and .0285 g (N=53 and 96); for females it was .1230 and .1489 mm and .0214 and .0282 g (N=81 and 109). Mean size and weight by month and season and a comparison of 1970-1972 juveniles by month (average SVL in mm) are indicated in Fig. 20-22. These monthly findings are based on the study plot population—except March, April, and May of 1970, whose data are based on field animals. Data indicate that for the entire season

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Fig. 20. Growth of hatchlings (1970-71) and juveniles (1970-72) by month. Vertical dotted lines represent 1970, horizontal lines 1971, and vertical lines 1972. Diagonal lines are estimates.

Fig. 21. Growth of male S. g. gracilis from hatchlings to adults (1970-71 combined). Dotted line represents weight; solid line, SVL.

Fig. 22. Growth of female S. g. gracilis from hatchlings to adults (1970-71 combined). Dotted line represents weight; solid line, SVL.
TABLE 9. Individual growth of juveniles in 1970 of known age. First figure shows weight in grams; second figure shows snout-vent length.

<table>
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<tr>
<th></th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
<th>Total Growth</th>
<th>Days Growth per Day</th>
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<td></td>
<td>2.29-39.0</td>
<td>4.67-51.0</td>
<td>5.06-52.0</td>
<td>6.32-55.0</td>
<td>2.77-13.0</td>
<td>72 .0384-1.805</td>
</tr>
<tr>
<td></td>
<td>4.92-43.0</td>
<td>2.59-43.0</td>
<td>4.05-46.0</td>
<td>5.45-55.0</td>
<td>1.40-12.0</td>
<td>80 .0175-1.500</td>
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<td></td>
<td>1.93-41.0</td>
<td>2.76-48.0</td>
<td>5.60-57.0</td>
<td>5.84-54.0</td>
<td>3.67-16.0</td>
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<td></td>
<td>1.62-32.0</td>
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<td>4.85-53.0</td>
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<td>5.19-53.0</td>
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<td></td>
<td>2.95-45.0</td>
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</tr>
</tbody>
</table>

through August males and females fluctuated in size. In the seasonal tally, males and females had essentially equal growth rates in 1970, and these juveniles were larger than 1971 juveniles in March and April. The May 1970 sample size was small and, therefore, an estimate was made for Fig. 20. This estimate was 39.9 mm SVL, which is intermediate between April and June of 1970. Using this estimate, the May 1970 growth rate seemed to be less than that of 1971. This lower growth rate is attributed to cool temperatures. However, in June 1970, juveniles again outgrew those of 1971. From July on, 1971 juveniles outgrew those of 1970. This higher growth rate results in an average 3.6 mm SVL greater size in August for 1971 juveniles.

Data for 1972 juveniles were incorporated in Fig. 20. These juveniles were larger than those of 1970 or 1971 in all months measured and attained the largest size (58.9 mm SVL) by August, an average of 5.5 mm SVL larger than 1970 juveniles and 2.0 mm larger than 1971 juveniles. The major factor is seemingly the greater number of days for growth (14 in 1972). If the average value for growth per day in 1972 juveniles is multiplied by 14 additional days of growth, the value attained is an increase of 2.07 mm SVL, an approximation of the 2.01 mm SVL difference in the two years. Another apparent reason for the larger size of 1972 juveniles compared to 1971 is a larger mean size at emergence (33.1 mm as compared to 31.6, a difference of 1.5 mm SVL) indicating the larger size of hatchlings in 1971. However, 1971 juveniles had a greater growth rate than 1972 juveniles (0.005 mm SVL per day). The 1972 season was one of the driest on record in Utah and on the study plot (Fig. 3). This undoubtedly affected the flora and arthropod population, and perhaps the growth rate of 1972 juveniles.

**Adults**

Data concerning adult growth are indicated in Fig. 21 and 22 and Table 10. The means for males and females of the study plot and those of other parts of Utah County are not significantly different, thereby allowing us to use the study plot animals to make inferences about Utah County populations.

In comparing first-year adults and older individuals of known age, study plot females were significantly larger than males (Table 10). This fact is also substantiated in the growth curves in Fig. 21 and 22, which also indicate that males have a reduced rate of growth in relation to females, particularly after the second hibernation.

Weight differences were not as great as they appear to be in Fig. 21 and 22. The large increase and decrease in the weight of females through the season, caused by the volking of eggs, made it difficult to compare the sexes on the basis of weight for the entire activity season. Female weights taken in July and August after eggs were deposited averaged approximately

**Table 10.** Comparison of SVL in adult males and females from Utah County collections and study plot records.

<table>
<thead>
<tr>
<th></th>
<th>Number</th>
<th>Range</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field males</td>
<td>106</td>
<td>52-63.0</td>
<td>57.39</td>
</tr>
<tr>
<td>Field females</td>
<td>121</td>
<td>53-69.0</td>
<td>59.91</td>
</tr>
<tr>
<td>Study plot males</td>
<td>59</td>
<td>54-63.0</td>
<td>57.82</td>
</tr>
<tr>
<td>Study plot females</td>
<td>62</td>
<td>54-66.0</td>
<td>60.59</td>
</tr>
<tr>
<td>Study plot first-year adult males</td>
<td>32</td>
<td>54-61.0</td>
<td>56.67</td>
</tr>
<tr>
<td>Study plot first-year adult females</td>
<td>38</td>
<td>54-63.0</td>
<td>58.65</td>
</tr>
<tr>
<td>Study plot second-year adult and older males</td>
<td>27</td>
<td>55-63.0</td>
<td>59.18</td>
</tr>
<tr>
<td>Study plot second-year adult and older females</td>
<td>24</td>
<td>58-66.0</td>
<td>63.47</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th>Total</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>27</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Average in g</td>
<td>6.36</td>
<td>7.16</td>
<td></td>
</tr>
<tr>
<td>Biomass in g</td>
<td>171.7</td>
<td>257.7</td>
<td></td>
</tr>
<tr>
<td>Total biomass in g</td>
<td>429.4</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

6.86 g per lizard (N = 46). Males averaged 6.36 g per lizard (N = 42).

There was a significant difference between the adult age groups of males and females, with older individuals showing a larger average size. The largest male measured (SVL) in Utah County was 66 mm and the largest female was 70 mm.

Density and Biomass

Estimated resident density and biomass (1971) for adults, juveniles, and hatchlings are provided in Tables 11, 12, and 13. The density for hatchlings was not calculated in the same manner as that of adults and juveniles. Only the number of hatchlings captured each month was used to compute density values. Recapture data were not used because few hatchlings were captured more than once. The biomass was calculated by using the average weight of the hatchlings captured each month, the totals depicting the approximate biomass added to the population from August through October. The total number of hatchlings captured is also given. The estimated resident density per hectare for adults and juveniles is provided in Table 14.

Sex Ratio

In 1971 the most complete data were available for both adults and juveniles on the study plot. These data (Table 15) were based on single captures per month of each group and not on recaptures. This was done in order to effect a random sampling of the population in Utah County, rather than to figure sex ratio fluctuation in an area where only one or two lizards were seen each day. Field data showed the sex ratio to be 1:1 during April, May, and early June, after which males are seen less often than females.

Estimated Potential Production and Survivorship

Data showing potential production of eggs on the study plot are listed in Table 16. The number of eggs is based on the average clutch size per female and the recaptures of individuals. The clutch size per female is provided in Table 17, and the number of recaptures is given in Table 18. The summary in Table 19 shows the total number of eggs produced and the average clutch size per female. The number of females in Utah County which might produce eggs is provided in Table 20, along with the number of juveniles and adults, and the total number of hatchlings. The data are given in Table 21 and are on the study plot.


<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th>Total</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1971 density</td>
<td>25</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>April mean weight</td>
<td>1.38</td>
<td>1.44</td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>34.5</td>
<td>44.6</td>
<td></td>
</tr>
<tr>
<td>May mean weight</td>
<td>2.39</td>
<td>2.17</td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>59.7</td>
<td>67.3</td>
<td></td>
</tr>
<tr>
<td>June mean weight</td>
<td>2.97</td>
<td>2.64</td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>66.7</td>
<td>81.8</td>
<td></td>
</tr>
<tr>
<td>July mean weight</td>
<td>4.33</td>
<td>4.16</td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>108.3</td>
<td>128.9</td>
<td></td>
</tr>
<tr>
<td>August mean weight</td>
<td>6.00</td>
<td>5.80</td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>150.0</td>
<td>179.8</td>
<td></td>
</tr>
<tr>
<td>August total biomass</td>
<td>329.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th></th>
<th>1970</th>
<th>1971</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>Average in g</td>
<td>.66</td>
<td>.72</td>
</tr>
<tr>
<td>Biomass</td>
<td>13.8</td>
<td>15.1</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>42</td>
<td>47</td>
</tr>
<tr>
<td>Average in g</td>
<td>1.00</td>
<td>.96</td>
</tr>
<tr>
<td>Biomass</td>
<td>12.0</td>
<td>45.1</td>
</tr>
<tr>
<td>October</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>20</td>
<td>11</td>
</tr>
<tr>
<td>Average in g</td>
<td>1.09</td>
<td>1.02</td>
</tr>
<tr>
<td>Biomass</td>
<td>21.8</td>
<td>11.2</td>
</tr>
<tr>
<td>Total number</td>
<td>81</td>
<td>76</td>
</tr>
<tr>
<td>Combined</td>
<td>162</td>
<td>246</td>
</tr>
<tr>
<td>number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>for each year</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total biomass</td>
<td>77.6</td>
<td>71.4</td>
</tr>
<tr>
<td>Combined biomass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>for each year</td>
<td>149.0</td>
<td>205.5</td>
</tr>
<tr>
<td>Grand total biomass</td>
<td>351.5</td>
<td></td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th></th>
<th>1970</th>
<th>1971</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>19</td>
<td>25</td>
</tr>
<tr>
<td>Animals ha</td>
<td>11.0</td>
<td>14.3</td>
</tr>
<tr>
<td>Sexes combined</td>
<td></td>
<td></td>
</tr>
<tr>
<td>animals ha</td>
<td>25.4</td>
<td>36.3</td>
</tr>
<tr>
<td>Animals ha</td>
<td>28.4</td>
<td>40.5</td>
</tr>
<tr>
<td>Juveniles</td>
<td>25</td>
<td>29</td>
</tr>
<tr>
<td>Animals ha</td>
<td>14.3</td>
<td>16.8</td>
</tr>
<tr>
<td>Sexes combined</td>
<td></td>
<td></td>
</tr>
<tr>
<td>animals ha</td>
<td>31.1</td>
<td>32.4</td>
</tr>
<tr>
<td>Animals ha</td>
<td>34.8</td>
<td>36.3</td>
</tr>
<tr>
<td>Study plot size</td>
<td>172 ha</td>
<td></td>
</tr>
<tr>
<td>Excluding uninhabited areas</td>
<td>155 ha</td>
<td></td>
</tr>
<tr>
<td>Animals ha for adults and juveniles in 1970</td>
<td>50.8</td>
<td></td>
</tr>
<tr>
<td>Animals ha for adults and juveniles in 1971</td>
<td>69.2</td>
<td></td>
</tr>
<tr>
<td>*Animals ha for adults and juveniles in 1970</td>
<td>63.2</td>
<td></td>
</tr>
<tr>
<td>*Animals ha for adults and juveniles in 1971</td>
<td>76.8</td>
<td></td>
</tr>
</tbody>
</table>
size of females in each age and/or size class found on the study plot in June and the first part of July who may have potentially laid a clutch at the study plot. As was expected, this potential production of eggs was greater than the total number of hatchlings captured. If the actual number of hatchlings captured in each year is compared with the number of potential eggs laid, there is an approximate egg and/or nest failure of 31.0 and 32.5 percent for 1970 and 1971. Hatching survival in 1970 was 24.7 percent and in 1971, 18.3 percent. The number of juveniles surviving to adulthood after the second hibernation was 36, or 81.6 percent.

### Life Table of S. g. graciosus

A life table is presented in Table 17. Since the population was not studied long enough to take one generation completely through its cycle, the values used for survivorship between first year, second year, and third year adult females were based on the proportion found in the population, with the fourth year given as an estimate. The X represents age classes (months), $L_x$ is survivorship, and $M_x$ is one-half the mean number of eggs that a female will lay in each age group. The sum of $L_xM_x$ ($L_xM_x$) is the $R_e$ (capacity for increase) .909. The $T_e$ (cohort generation time) is calculated by dividing $XLM_x$ by $L_xM_x$. In the case of S. g. graciosus, cohort generation is approximately 30.13 months.

### TABLE 16. Estimated potential production for 1970 and 1971 as compared to actual numbers of hatchlings captured. Survivorship of hatchlings to juveniles and juveniles to adults. Based on study plot data.

<table>
<thead>
<tr>
<th>Potential production</th>
<th>1970</th>
<th>1971</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number marked</td>
<td>162</td>
<td>246</td>
</tr>
<tr>
<td>Estimated nest failure</td>
<td>31.0%</td>
<td>32.5%</td>
</tr>
<tr>
<td>Hatchlings surviving to next year</td>
<td>44 (27.1%)</td>
<td>45 (18.3%)</td>
</tr>
<tr>
<td>Hatchling mortality</td>
<td>72.9%</td>
<td>81.7%</td>
</tr>
<tr>
<td>Estimated number of juveniles surviving from 1970 to adults in 1971</td>
<td>36 (81.8%)</td>
<td></td>
</tr>
<tr>
<td>Mortality of juveniles</td>
<td>18.2%</td>
<td>18.2%</td>
</tr>
</tbody>
</table>

### TABLE 17. Estimated life table of S. g. graciosus in Utah County, Utah.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>$L_x$</th>
<th>$M_x$</th>
<th>$L_xM_x$</th>
<th>$XLM_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>123.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>11.0</td>
<td>27.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>23.0</td>
<td>21.6</td>
<td>2.8</td>
<td>60.48</td>
<td>1391.0</td>
</tr>
<tr>
<td>35.0</td>
<td>7.2</td>
<td>3.2</td>
<td>23.04</td>
<td>806.4</td>
</tr>
<tr>
<td>47.0</td>
<td>1.8</td>
<td>3.9</td>
<td>7.02</td>
<td>329.9</td>
</tr>
<tr>
<td>59.0</td>
<td>0.9</td>
<td>4.0</td>
<td>3.60</td>
<td>212.4</td>
</tr>
<tr>
<td>90.90</td>
<td>100</td>
<td>R_e</td>
<td>2739.7/100 = T_e</td>
<td></td>
</tr>
<tr>
<td>90.90</td>
<td>100</td>
<td>R_e</td>
<td>T_e = 27.30</td>
<td></td>
</tr>
</tbody>
</table>

Cohort generation time ($XLM_x$) = 30.13 months

### DISCUSSION

Sceloporus g. graciosus is commonly found in the upper Sonoran and Transition life zones in Utah County, Utah, and Woodbury and Woodbury (1945) found it in this same habitat in Salt Lake County. The sagebrush swift requires open, well-illuminated areas between scattered vegetation. The Utah County population was found primarily at elevations of 1,371 to 1,829 m, and records of other collectors indicate that S. g. graciosus may occur at elevations higher than 1,829 m. The study plot population was at approximately 1,495 to 1,569 m. When found at higher elevations, they occurred principally on south-facing slopes covered with oak-maple and sagebrush, juniper-pinyon, and sagebrush, or combinations of these.

Woodbury and Woodbury (1945) stated that S. graciosus was first noticed in April, and Mueller (1969) reported that Yellowstone populations did not appear until May. Stebbins (1944) observed them first in late May in California, while activity of Utah populations begins in March.

In 1970 and 1971 sagebrush swifts appeared on 20 and 22 March, and in 1972 they were first observed on 5 March. Adult males and juveniles of both sexes appeared first in all three years, with adult females emerging later. Adult males appeared an average of 16.3 days earlier than females, which allows them time to set up territories. Woodbury and Woodbury (1945), Newman and Patterson (1909), and Noble and Bradley (1933) stated that other members of the genus Sceloporus also establish territories before females emerge. Two additional reasons explaining the early emergence of males might
be the noticeable reduction in fat body size (Fig. 17) at the time of emergence as compared to before hibernation, a stimulus to emerge and seek food. Also, males may tolerate lower temperatures than females and would thus be activated at lower temperatures resulting in earlier emergence. Firm evidence for the second reason is not available, however, as both male and female juveniles emerge with adult males. Juveniles are about one-sixth the size of adult males in late March and should warm faster and adjust to short periods of sunshine in the early spring. A positive reason for the early emergence of adult males is not known. We only suggest that a need for food and temperature relationships are possible stimuli.

Sagebrush swift temperature relationships pose several questions when compared to the studies of Brattstrom (1965), Cole (1943), Cowles and Bogert (1944), Larson (1961), Mueller (1969), and Tanner and Hopkin (1972). Average lizard temperatures of March were the lowest for the activity season (Fig. 4): they continued to increase until they reached their highest average in early August, which was also the period with the highest air temperatures (1 m and 3 mm). Mueller (1969) also observed a similar temperature relationship for Yellowstone National Park populations, in which the average temperatures of lizards increased along with the average environmental temperatures. However, average temperatures in Utah populations are seemingly higher than those for Yellowstone populations, possibly the result of adaptation to the lower average temperatures resulting from greater elevation and latitude. Brattstrom (1965) suggests that the average body temperature is in inverse relationship to increasing altitude. This relationship appears to be true in contrasting Yellowstone and Utah populations, with the exception that Utah populations do not follow Brattstrom’s curve.

Juveniles emerging from their first hibernation follow essentially the same daily temperature increase as adults (Fig. 4) from March through May, even though they are much smaller. Hatchlings cannot endure exposure to temperatures above 36 °C. Perhaps there is a lag in the development of temperature control mechanisms, which are gradually developed in juveniles. The small size of hatchlings may allow for a rapid heating or cooling of the body, causing rapid body temperature fluctuations which may be critical if not controlled. In mid-August daily temperatures may be high; however, nights begin to cool and the average daily temperature turns downward. It is at about this time that fewer adults are seen. By September hatchlings have averages essentially the same as those of the remaining adults and juveniles, indicating an attainment of temperature control.

Adults and juveniles emerged from retreats at temperatures of 16 to 21 °C, comparing closely with the observations of Tanner and Hopkin (1972) for Sceloporus occidentalis loricatus at 15 to 20 °C. Critical thermal maxima (CTMax) for adult lizards from the study plot are close to those found by Mueller (1969) for Yellowstone populations averaging 43.6 °C (spring), 42.6 °C (summer), and 43.4 °C (fall).

In all age classes (Fig. 4) the mean body temperature for each month was higher than air temperatures at 1 m and 3 mm above the substratum. Mueller (1969) reported similar findings in Yellowstone National Park; however, his air and substratum temperatures were taken one inch above the surface and at the surface. Mueller compared these two temperatures and found them not significantly different; however, he states the possible reason for such equality to be thermal activity and lack of air mixing at the surface because of rough substratum material. Cowles and Bogert (1944) and Larson (1961) found mean cloacal temperatures to be intermediate between substratum and air temperatures, with substratum being higher.

It is difficult to compare temperatures of Utah populations with others because of the methods of measurement; however, it can be stated that lizards have a higher temperature than substrates up to June and again in September. During the intervening months, few, if any, lizards were found abroad during the hot periods of the day (Fig. 5). In June, July, and August, lizards have higher body temperatures in the morning and lower during the afternoon, when the substrate has warmed. This is in contrast with Mueller (1969) and Cowles and Bogert (1944), who indicated body temperatures are greater than or intermediate to the air and substrate.

Another aspect of thermoregulation is related to the acquiring of body heat either from substrate, radiant heat, or both. Mueller (1969) believes that direct radiant energy is the primary source, but that substrate is utilized when radiant energy is unavailable. He based this on data indicating higher lizard temperatures than either air or substrate. This is in contrast to Cole (1943), Cowles and Bogert (1944), and Larson (1961), who stated that substrate is the primary source. Observations of Utah populations lead us to conclude that radiant energy is the primary source for warming in the morning (basking) before the substrate temperatures (which
increase much more slowly) reach the appropriate temperature for lizard activity. For example, thunderstorms cool the air and substrate; however, after a storm, lizards are out basking. It is unlikely that this warming came primarily from substrate, even though the lizards were on rocks. Tamer and Hopkin (1973) observed *S. occidentalis longipes* emerge and warm to an optimal temperature by basking while the temperature of the morning air was still cool. It is presumed that the substrate temperature was also cooler than the lizards when they reached their optimal temperature. Their general conclusion is that solar energy provides the prime source of body heat.

By flattening the body against the substrate, lizards eliminate circulating air under the body and thus speed up the process of heating. This flattening also increases the surface area of the body directed toward the sun. While some heat may be conducted from the lizard to the substrate, in full sun this is much less than that received. Interestingly, *S. gracilis* does not darken the surface of the body as *S. o. longipes* does in order to increase warming. Activity begins once the preferred temperature is reached. As air and substrate temperatures continue to increase during July and August, lizards avoid excessive heat by seeking shade and reducing activity. It was our observation that lizards utilize radiant heat first and use substrate only when the former is unavailable.

The mean preferred temperature for adults and juveniles in Utah County was 32.8° C, which is between that reported by Mueller (1969) for *S. g. gracilis* (30.9° C) and by Brattstrom (1965) for *S. g. vandenburghianus* (37.5° C) and *S. g. gracilis* (34.9° C).

In March, lizards were active for 6 to 7 hours per day (Fig. 5). This time gradually increased to 12 or 13 hours per day in June, July, and August. September activity decreased to 7 or 8 hours per day for adults and juveniles, and 9 or 10 hours for hatchlings. Pianka and Parker (1972) noted this behavior in *Callisaurus draconoides*. Stebbins (1944) reported two periods of activity during the day for *S. g. gracilis*. Utah populations also manifest this bimodal activity.

Stebbins stated that the late afternoon peak was from 1400 hours to 1700 hours Pacific standard time. Utah populations have a late afternoon peak centering around 1700 hours to 2000 hours mountain standard time, which is approximately two hours later than that of California populations. A possible explanation for the lag in activity peaks is their geographical location. Stebbins's study of *gracilis* took place at 1,829 m in a conifer forest in Mt. Lassen Volcanic National Park, whereas Utah populations were at 1,524 m in a scrub oak-maple, sagebrush association. Pianka and Parker (1972) indicated this same separation of activity during the hottest period of the activity season in *Callisaurus draconoides*. Mayhew (1964, 1968), Pianka (1969, 1971), and Tinkle (1967b) have also reported these seasonal shifts.

The development of this bimodal activity is apparent from June through August and is probably necessary to keep the body temperature from reaching a critical level. This intermediate period of reduced activity with an activity temperature may also facilitate digestion of food gathered in the early morning and thus provide for reproduction in June and fat body build-up in July and August before hibernation.

Bimodal activity was also manifest in hatchlings in August (Fig. 5). The retreat from high afternoon temperatures by hatchlings is explained by their apparently lower tolerance for high temperatures. In adults, juveniles, and hatchlings the late afternoon peak is probably triggered by the reduced temperature from 1600 hours into evening. Late afternoon activity was not as great as the morning activity peak.

According to Stebbins (1944), *S. g. gracilis* seeks well-illuminated areas and their seasonal activity may vary with the changes of the incident rays of the sun. *Sceloporus g. gracilus* activity also appears to be affected by the incident rays and the slope of the habitat they occupy. Slope preference was observed on the study plot, an area nearly ideal for slope exposure. The south-facing slope was frequented most by all age classes throughout the activity season, except juveniles in September (Table 1). This preference is explained by the following factors: first, it has the most continuous exposure to sunlight (highest temperature) throughout the year. Second, it supports more open areas, which seem to be preferred by the lizards (Stebbins, 1944). Third, it offers a better place for incubation of eggs (Rand, 1972).

Seasonal fluctuations in activity are explained primarily by the angle of exposure, which affects temperature and ultimately the ability of lizards to warm up to an activity temperature. In March, adults and juveniles were absent from north- and west-facing slopes. March temperatures were sufficiently high to bring lizards out of hibernation on the south slope, but none were seen on other slopes. By mid-April adults were found on all slopes, but not in the same abundance as south slopes.

Exposure and temperature exert a considerable effect on hatchlings, as evidenced by
Behavior

Behavior is expressed in individual actions and interactions between two or more individuals. Individual lizards were observed feeding in the field and in captivity. As prey items increased in size, they were grasped and shaken more vigorously. Hatchlings were able to recognize prey within an hour after hatching and exhibited the same shaking of prey as adults and juveniles, suggesting that the feeding reflex is inherent.

Aggression was observed in and between all age groups, within and between sexes. In females it was manifested by arching of the back, sides compressed, limbs extended, and the tail pointed upward. Stebbins (1944) also observed this in gracilis and referred to it as an act of intimidation. Noble and Bradley (1933) noted this behavior in S. undulatus females in addition to their hopping on stiff limbs. Hopping was observed once in graciosus in a situation where a juvenile male approached a gravid female. The same general pose was observed when an adult male approached a female that had previously copulated and also when a captive female opposed other females that tried to take away her prey. This behavior is apparently a general pattern followed by adult females and may represent a rejection display. It was not noticed in hatchling females or small juveniles.

Aggression in males was usually manifest in a defense of their territory during the breeding season. The color and pattern of the adult male body is considered necessary for males to recognize each other and elicit aggressive behavior. This was noted by Tanner and Hopkin (1972) for S. o. longipes, along with head bobbing. Head bobbing was not noticed in S. g. graciosus when the combatants were close to each other. The general aggressive pattern was compression of the sides and lowering of the dewlap, with the body extended high on the limbs. This pose was presented laterally to challenging males but not to females. Primarily it was a bluff against intruders, though fighting males were observed in the field as well as in captivity, with the resident male always dominant over an intruder or challenger. Juveniles and hatchlings were observed chasing intruders of both sexes from areas they were occupying. Adult males also removed juveniles from their territories.

Panting by lizards was observed in the field and in captivity. It is apparently an emergency behavior used when the body temperature is approaching a critical level. Critical thermal maxima studies substantiate that panting takes place just prior to reaching the maximum level.
tolerated by the lizard. Mueller (1969) also noticed this behavior.

Pushups were observed in all age classes by both sexes. It seems an inherent behavior necessary for the survival of the population because of its apparent relationship to species identification; consequently, reproduction and other social interactions depend on it.

Reproductive activity is a most important behavior. Courtship activity in April and the first part of May is preliminary and does not result in copulation. The general sequence of events leading to copulation is as follows: the male becomes aware of the female, approaches her with his head bobbing very rapidly, and then, as he reaches the female, grasps her on the neck or shoulder region with his mouth, pauses for a short time and assumes a dominant position over the female's body (a period of usually less than 30 seconds). The male then thrusts his vent into contact with that of the female. At this same time the hemipenis is inserted into her cloaca. Woodbury and Woodbury (1945) describe the male as holding the female with the front and hind limbs; however, in Utah County populations only one of each pair of limbs could be considered as holding the female (Fig. 7C).

The hemipenis undergoes rhythmic contractions while inserted, with duration of copulation only five to ten seconds. Woodbury and Woodbury (1945) state that grasping of the neck does not occur with S. g. gracilis. In all the copulations observed, the neck or shoulder grasping was a necessary behavior in order for the male to remain secure. Noble and Bradley (1933) substantiate this in their studies on several species of Sceloporus.

Escape behavior usually consists of a retreat to bushes, holes, or rock crevices. Individuals have been observed retreating into heavy leaf litter and playing dead. This appears to be an alternative to running from the predator. Lizards manifesting this behavior, particularly the smaller ones, were difficult to find and often escaped capture.

Tail thrashing and vibration were exhibited when lizards approached large prey, when they were captured by hand, and, in males, during precopulatory activity. This behavior is suggested of a nervous response and may be an example of a ritualistic type of behavior (Goin and Goin, 1971).

Food

Knowlton, Maddock, and Wood (1946) analyzed the stomach contents of S. g. gracilis from various populations in Utah and provided a list of food, by orders and families, similar to the food items listed in this study. Food analyses indicate that the staple food throughout the activity seasons of 1970 and 1971 consisted of Hymenoptera (mostly Formicidae), which made up 2,506 of 3,807 items taken in 1970 and 1,980 of 3,367 items in 1971, and Coleoptera (Table 2), which made up 353 of 3,807 in 1970 and 399 of 3,367 in 1971. These data compare with Tanner and Hopkin (1972) and Tanner and Krogh (1973), who stated that S. o. longipes and S. magister fed mainly on ants and any other small arthropods that were in abundance. Stebbins (1944), working on S. g. gracilis, found that carpenter ants were the most abundant in the few stomachs they examined.

Before juveniles reach adult size they are eating essentially the same prey as adults, in the same priority, and apparently of the same size. Davis (1967) agrees, stating that as S. occidentalis juveniles reach adult size they eat the same prey items as adults, becoming competitive for the food supply. Similar competition was apparent in S. g. gracilis before adults retired in August. Since hatchlings appear in August and utilize smaller prey in smaller quantities than adults or juveniles, it is doubtful they provide competition.

The sagebrush swift is not an extremely selective feeder (Table 3) but, rather, an opportunist whose diet tends to fluctuate monthly as different insects and other arthropods appear. There may also be yearly fluctuations based on the greater number of arthropods present in one year than in others. Fluctuations in flowering time for various floral types also affect the arthropods present throughout the activity season.

Hymenoptera and Coleoptera were the prey most often eaten by adults and juveniles in 1971. Hatchlings fed predominately on Formicidae (Hymenoptera), small Coleoptera, Homoptera, and Arachnida.

Tanner and Hopkin (1972) noticed that S. o. longipes does not appear to move about foraging for food but basks in the sun and loafs in the shade, eating available arthropods of suitable size that attract attention. In contrast, S. g. gracilis does forage for food and was observed feeding in the scrub-oak maple thickets and in sagebrush during the morning activity peak. However, during hotter periods of the day these behaved as S. o. longipes. Tanner and Hopkin also noticed materials such as rocks and plant parts, feathers, red plastic, pinyon needles, etc., in the stomachs. Rocks and plant parts were found in S. g. gracilis stomachs, but other materials were not. The rocks and plants were probably ingested accidently while capturing
prey, or the plants were possibly moving in the wind and were mistaken for prey.

The sexes differed in variety of food items consumed. Adult and juvenile females consumed more Hymenoptera (mainly Formicidae) than did males. Most other orders were consumed in equal numbers. The average number of items per male and female would suggest that males, being more aggressive, ate larger prey and therefore fewer items than females. This dichotomy was not found in hatchlings.

Another factor in food relationships was the difference between numbers and volume of prey items. In Callisaurus draconoides (Pianka and Parker, 1972) the frequency of a particular order utilized may be high while the volume is not. It is possible that volume is a better indicator than number of items. Order of priority for staple food items by volume is different from that by frequency. For adults it was Coleoptera, Hymenoptera, Orthoptera, Lepidoptera and Arachnida in descending order; for juveniles, Arachnida, Coleoptera, Hymenoptera, and Lepidoptera; for hatchlings, Hymenoptera, Arachnida, and Lepidoptera. It is very likely that caloric studies would prove more enlightening than either frequency or volume studies.

In some cases stomachs were completely filled with certain insect orders, again indicating the opportunistic feeding of S. g. graciosus. They appeared to rely on sight for finding prey, in contrast to Cnemidophorus hyperythrus beldingi, which, according to Bostie (1966a), uses olfactory senses for procuring food.

From the standpoint of practical importance, Knowlton, Maddock, and Wood (1946) stated that S. g. graciosus is an important predator of insect pests which compete with livestock for forage and also of insects which multiply in range land and then migrate to nearby cultivated fields. This also applies to Utah County populations. It is our conclusion that graciosus as well as other insectivore species are economically important and a necessary link in the Great Basin ecosystem.

Parasites

Stebbins (1944), Knowlton, Maddock, and Wood (1946), and Woodbury (1934) have noted nematode parasites in the stomachs of S. gracilis from California and Utah. No nematodes were observed in the 385 stomachs of lizards from Utah County. In 690 stomachs removed from lizards for food analysis, we observed only two tapeworms (Oochoristica scelopori). The presence of nematodes in Utah populations outside of Utah County suggests geographical isolation or that appropriate intermediate hosts are not present (Pearce and Tanner, 1973).

Ectoparasites were found mainly on lizards collected from West Canyon in northwestern Utah County. Ticks (Ixodes) in both larval and nymphal stages were found in April and May. In July and August mites (Trombiculidae) were also found mainly on lizards from West Canyon. This suggests that ticks and mites are prevalent at different times of the year and tend to be localized; therefore, lizards occupying some areas may have a higher incidence of infestation than others.

Predation

Predation was not witnessed in the field at any time. Suspected predators are Coluber constrictor, Mastigophis taeniatus, and Pituophis melanoleucus when sympatric. Hypsiglena torquata is a known predator in Utah County. The sparrow hawk occurs in the same habitat and is known to prey on Cnemidophorus tigris in Utah County (Smith, Wilson, and Frost, 1972) and Phrynosoma platyrhinos in southern Nevada (Tanner and Krogh, 1973). It is therefore considered to be a possible predator. Crotaphytus collaris has been observed preying on gracilis in captivity. Taylor (1912) reports a Crotaphytus wislizenii preying on gracilis in Nevada, and, since both species are found in Utah County, they are considered possible predators.

Tail ratios and breakage

As lizards grow, the ratio of tail length to body length increases (Fig. 8). Mueller and Moore (1969) noted this for the Yellowstone population and Blair (1960) observed similar changes in S. olivaceus. Our data also indicate that the proportion of tail to body length is greater in males from the time they reach approximately 50 mm SVL. In both sexes there is a reduction of the ratio after reaching approximately 60 mm or more. S. olivaceus does not show the reduction of relative tail length. The difference in tail ratio of male and female S. g. gracilis may be caused by the portion of the tail occupied by the hemipenis. In adult males (54-60 mm SVL) this amounts to an average of 63 mm. Blair states that males have longer tails because they do not carry eggs. He also considers natural tail breakage in olivaceus as an indicator of predation in the population. However, fighting between adult males during the breeding season (to protect the activity center) and certain situations where the male may grasp the tail of the female during copulation may also result in tail breakage. The percentage of tail breakage in gracilis increased with age. Blair
concludes that males have a higher predation rate than females because of coloration, display, home range patrolling, and mating activity. Also, males have a greater ability to elude predators, based on the high percentage of tail breaks. It would seem that the greater ability to elude would result in less predation, and not in a significantly greater density of females as Blair reported for S. olivaceus. S. g. gracilis and S. olivaceus males have a higher percentage of tail breakage and perhaps predation than females. Gravid females are orange laterally and less agile until the eggs are laid. It was our observation that males and females are almost equal in attracting predators. Two possible reasons for the differences in the percentage of tail breakage in males are that they are more aggressive and they emerge earlier. This probably contributes to a higher predation rate and may be responsible for a slightly greater density in females (8 percent). In S. olivaceus females are significantly (statistically) more abundant. In comparing the Utah County population with Blair’s population in Texas, it was concluded (based on natural breaks as an indicator of predation) that predation of northern forms is less than that of southern forms. Pianka and Parker (1972) observed this in Callisaurus populations ranging from central Nevada to Estero de Tastiotla, Sonora, Mexico. Pianka (1965 and 1970) reported similar latitudinal shifts in Uta stansburiana and Cnemidophorus tigris. Studies of southern populations should be undertaken to test if this is true in S. gracilis.

In tail regeneration, color pattern and certain colors (blue greens in males and orange in females) were not present in the regenerating portion, only a uniform ground color. This suggests that the cells producing the colors were absent. The regenerating portion was also lighter ventrally. Stebbins and Robinson (1946) reported this same phenomenon in California populations of S. g. gracilis. Data were not available to make conclusions concerning advantages or disadvantages in the lack of color and pattern.

**Age groups and Reproduction**

Females were considered adults if they contained yolking follicles, ovudical eggs, or corpora lutea. The minimum age of reproductive females is 22 to 23.5 months.

Hatching females show an increase in number and size of follicles as they grow. Tinkle (1961) found this same situation in Uta. Follicle growth continues during their juvenile year until June and July (Table 3). The reduction in follicle size in juveniles is possibly caused by greater activity, heat, fat deposition, and diet during May, June, and July. Overall, the average number of follicles increased from the time of hatching and reached a plateau (average) of 18 follicles per female in the second reproductive year. The phenomenon of producing more follicles than can be developed and laid in one breeding season appears to be a general characteristic in saurians. It appears to occur in Sceloporus, and Tanner (1957) observed it in Eupeps.

In adult females unyolked follicles exhibit some seasonal fluctuations (Table 4 and Fig. 9), with decrease in size and numbers of follicles occurring during the breeding season. The reason for a reduction appears to be the use of lipids and fats contained in the unyolked follicles for yolk deposition, similar to their use in fat bodies (Hahn and Tinkle, 1965). The increase in number and size of unyolked follicles after the breeding season may be in response to the build-up for the next year.

Yolk deposition started in late August and the first part of September in adult and juvenile females, just before they retired for the season. These follicles were 1.9 to 2.0 mm in diameter and began to appear yellowish. Activity in the ovaries apparently ceased during hibernation. Meiosis was observed in S. o. longipes collected in August and September from Nevada. Woodbury and Woodbury (1945) state that female gracilis entering their second hibernation (juveniles) had ova that were enlarging (2-3 per lizard). Our data suggest that not all females (adults or juveniles) were undergoing meiosis in August and September or had large, yellowish follicles, though all showed increased size of follicles (Tables 3 and 4, Fig. 10). After yolk deposition is well underway in the spring, ova increase rapidly in size. Ovulation took place when ova averaged approximately 7.09 mm in diameter and 21 g in weight. The majority of this growth takes place over a period of about 60 days. Data from a female captured in the process of ovulation indicate that the process of ovulation and passage into the oviducts is rapid and probably lasts no longer than twenty-four hours. The period of ovulation appears to occur as females reach their most brilliant nuptial color. Apparently copulation precedes ovulation, thereby avoiding the obstruction of sperm by eggs that have already passed into the oviducts.

Transcoelomic migration of ova has been observed in various species of reptiles (Legler, 1955; Tinkle, 1961; Mayhew, 1963, 1966a, 1966b, and 1971; Bostic, 1966b; Hoddenback, 1966; and Burkholder and Walker, 1973). In S. g. gracilis, the ova have a migration rate of about 42
percent (48/20). There seems to be a limit of 4 or 5 ova per oviduct, and, therefore, migration does not occur after an oviduct has received this number. This percentage is higher than that recorded in other reports, except that of Hoddenback (1966), who reported 66 percent in five individuals of Cnemidophorus sexlineatus. Telford (1969) criticizes Hoddenbach for his small sample size, and yet 50 percent or more does not seem impossible. The physical features of the ecelomic cavity suggest a passage of ova into the adjacent oviduct in all cases. Hoddenbach (1966) suggests that the stomach position on the left side might cause a movement of ova from the left ovary to the right oviduct. In graciosus, movement is from left to right, and it would seem that a full or empty stomach may have an effect on ova migration.

Corpora lutae in S. g. gracilis disappear rapidly after oviposition. This is similar to reports on Uta, S. orcutti, and Uma species. In Takydromus studied by Telford (1969), however, corpora lutae persist for the life of the female.

The left and right ovaries produced an equal number of eggs (Table 7). This is similar to Johnson's (1960) and Mayhew's (1965, 1966a, and 1966b) findings in Holbrookia texana and Uma spp.

Approximately 13 percent of the females examined had atretic follicles. Tinkle (1961) found 10 percent as a maximum in Uta stansburiana. Atretic follicles in S. gracilis were present during and after the active season of egg production. In contrast, Telford (1969), Hoddenbach (1966), and Tinkle (1961) reported on the period when atretic follicles occurred in T. takydromus, Cnemidophorus sexlineatus, and Uta stansburiana. In Takydromus takydromoides atretic follicles were present only in the postactive season, whereas C. sexlineatus and U. stansburiana were seen only during the active season.

Based on counts of corpora lutae and oviducal eggs, there were no cases of partial oviposition observed. Females had either laid the entire clutch or all remained within the female. Recently oviposited eggs averaged 13.7 x 7.9 mm, which is larger than those reported by Van Denburgh (1922) at 13 x 7 mm. Grinnell, Dixon, and Linsdale (1930) reported a length of nearly 10 mm. Females that had just oviposited lost between 2.24 and 2.72 g. of body weight, a loss of about 36 percent. Females measured (SVL) less than 10 days after they had oviposited were shorter (6) or equal (2) to their size before oviposition (Table 6), suggesting that females carrying a clutch of eggs possibly increase their length by relaxing the ligaments and muscles in the axial skeleton. Approximately two weeks after females had laid eggs they were gaining weight and had reached their approximate previous length.

Sceloporus gracilis in Utah County lays one clutch of eggs per year. In contrast, Tinkle (1973) reported two clutches (4.2 eggs each) in southern Utah. However, his evidence is inconclusive since he states that only 1 of 72 females examined had both corpora lutae and ova undergoing vitellogenesis. This fact would cast considerable doubt on all life table studies based on two clutches per year. We recognize that an occasional year with an early warm spring may permit some females to produce two clutches. Also, those populations in the southern limits of the range may be more likely to produce two clutches. In Utah our three-year study has not convinced us that two clutches occur often enough to be an important factor in the fecundity of these populations. Fitch (1970), reporting on northern (Washington, Oregon, and Idaho) and southern populations (California and Baja California), found them laying single clutches averaging 3.60 and 4.21 eggs, respectively. The average clutch size for Utah County populations was 6.03, as determined from 143 clutches. This was significantly larger than the size reported by Fitch (loc. cit.) but similar to the clutch size of five or six eggs reported by Woodbury and Woodbury (1945) for Salt Lake County populations. Muelleer and Moore (1969) reported 3.2 eggs per female in Yellowstone Park populations. These females were only 47 to 51 mm SVL, which is significantly smaller than mature females in Utah County. The maximum size of Yellowstone females was 56 mm SVL. This compares well with the observations of Stebbins (1944) on S. g. gracilis, which had a maximum size of 57.5 and a mean clutch size of 3.3 (Stebbins and Robinson, 1946). In addition, Yellowstone and California populations had approximately 150 to 160 days of growth. Comparing these populations with those of Utah County, the mean clutch size in Utah was almost double. Furthermore, females reached a greater maximum SVL (70 mm) and had approximately 185 days for growth. Length of the growing period limits the average SVL attained by individuals in the population, and this size limitation directly reduces the clutch size. This appears to be a general relationship in Sceloporus lizards (Tanner, 1972; Davis, 1967; and Blair, 1960).

Clutch size increases as females grow in size. In Fig. 11 the first two categories approximate first-year reproductive females, with the third
category being second-year and the fourth category being third- and fourth-year reproductive females. Hoddenbach (1966) and Johnson (1960) reported that there was no difference in size of clutches as females increased in body size in *Chinidophorus sexlineatus* and *Holbrookia texana*. However, Blair (1960) considered clutch size to be a function of size and age. In his study, increased size was considered more important than age for first-year females. First-year individuals had a greater variation in size (SVL) than older individuals; also, larger first-year females produced larger clutches.

Some researchers indicate there is a relationship between size of eggs within a clutch and number of eggs to the size of the female. Tinkle (1961) believed that larger clutches had smaller eggs. Telford (1969) reported that, in *T. takydromoides*, the larger the female the larger the clutch and the larger the individual eggs. In *S. g. graciosus* neither of the above consistently occurs. It seems that the size of eggs depends on the fat stores and food availability in the particular niche where the female is living, regardless of age or body size (Table 5).

The incubation period in *S. g. graciosus* was approximately 48 days, with a range of 44 to 52, based on field and laboratory data. This is a shorter period than the 62 days reported by Woodbury and Woodbury (1945). The assumption that the incubation period is only from oviposition to hatching may not be entirely true. Fertilized eggs in laboratory animals were in the oviducts about 22 to 27 days. Adding part of this time to the above incubation period gives a more accurate time of 65 to 70 days from the time of fertilization (if fertilization occurs as ova enter the oviduct) to the time of hatching.

The gonadal cycle of females in 1970 was approximately 15 days later than in 1971. This lag between years is explained by fluctuating factors in the environment. Since 1970 and 1971 individuals emerged at about the same time, emergence time should have been a minor factor. However, prevailing weather conditions in the late spring in the form of cold fronts and possibly inadequate food supply appeared to be the most important factors. This same lag was also evident in the male gonadal cycle.

Males were considered sexually mature if they were 52 mm SVL or greater by 1 July. This is 2 mm greater than reported by Stebbins and Robinson (1946) for *S. g. gracilis*. Woodbury and Woodbury (1945) reported that the male testicular cycle reached its peak volume in late April and May and then dropped to its lowest level in July, picking up again before hibernation. They reported that gonads did not enlarge during hibernation, an observation at variance with our data, in which some increase in the diameter of seminiferous tubules occurred (Fig. 12). A slight increase in tubule size would partially explain the failure to notice changes when using volume measurements, suggesting a weakness in using them. Using the volume of testis as a criterion for lack of change during hibernation or any other period is an example. In addition to an increase in tubular size, there was a significant change in testicular weight during hibernation (Fig. 13). Another evidence for change in the testis during hibernation was the stage of the tubules at the time of hibernation as compared to that at the time of emergence, indicating that changes during hibernation are not apparent from volume studies. Other basic trends of the spermatogenic cycle of Utah *graciosus* are in agreement with the findings of Woodbury and Woodbury (1945).

The general trends in the gonadal cycle of male *S. g. graciosus* follow that reported for *S. occidentalis longipes* in Nevada (Tanner and Hopkin, 1972), but are in contrast to the cycles in *Uma* spp. and *Dipsosaurus dorsalis* reported by Mayhew (1965, 1966a, 1966b, and 1971). The differences are in the time of year and the duration of each stage. These variations appear to be caused by the locations of the populations and the length of the growing seasons.

One significant adaptation is the presence of spermatozoa in the epididymis for a period of 1.5 to 2 months, apparently essential to ensure insemination of females. Natural selection seemingly would favor the use of energy required to keep the sperm viable in the epididymis before and after the copulation period to insure a maximum number of inseminated females.

In 1971 we noticed that the pre-anal area of males was moist during the breeding season. To our knowledge this has not been previously described. The area was moist for approximately 45 days from the last of May to the first of July, overlapping and continuing after the copulation period. The use of this secretion is unknown. It is undoubtedly associated with reproduction, since it coincides closely with it, and may be a pheromone used as an attractant to females, or a lubricant used during copulation (Burkholder and Tanner, 1974).

Halm and Tinkle (1965) studied postecological fat body cycles in relation to reproduction in *Uta stansburiana* and found a definite usage during yolk deposition. Fat bodies in *S. g. graciosus* males were smaller than those found in females as a percentage of body weight (Fig. 16 and 17). This compares well with their findings for *U. stansburiana*; however, *S. graciosus*
had smaller fat bodies (percentage of body weight). The cycle followed by U. stansburiana was also different than S. gracilis, which may be explained by latitudinal differences and length of growing period in the two populations. In addition, U. stansburiana in Texas laid more than one clutch of eggs per year whereas S. gracilis in central Utah laid one. In U. stansburiana and Cnemidophorus sexlineatus (Hahn and Tinkle, 1965; and Hoddendehn, 1966) the fat body was used to provide energy for the first clutch only. Males used most of their post-hibernation fat body for general activity (i.e., courtship, home range patrolling, and defense of activity center) as suggested by Hahn and Tinkle (1965). Males and females began to replenish their fat bodies in late June when reproductive activity had ceased and only a few females still had oviducal eggs. In females, yolk deposition seemed to provide the greatest drain on fat bodies. In July males and females weighed essentially the same and had fat bodies of approximately the same size. By August and September males lagged in fat body buildup, suggesting that the next reproductive cycle was beginning.

Fat bodies in southern populations were not used in hibernation, according to Hahn and Tinkle (1965). In contrast, central Utah populations must retreat for a period of six months. Even though metabolism is very low, a certain amount of energy is needed and fat body stores are considered the main source of support. A comparison of fat body weights of September individuals with those recently emerged in March and April showed a decrease of 1.9 in males and 1.1 percent in females, which was apparently used during hibernation. The greater loss in males was perhaps the result of continued enlargement of the gonads during hibernation (Fig. 16 and 17). Females do not follow precisely this cycle because most of their reproductive activities occur in the spring. If hibernation curtails most metabolic activity, except for survival, gonad size and tubule diameter in males should be similar between entrance into hibernation and emergence. Fat bodies in males should also be similar to that of females.

Although there was less than a 10 percent overlap in fat body data for juveniles and adults in August and September, the basic relationships between juvenile males and females are obvious. Even though juveniles increased equally in body size (SVL) and weight, female fat bodies grew faster than those in males from mid-July through September. The size of fat bodies in juvenile females increased over that in males from mid-July to September for the same reasons observed in adults. Hatchling fat bodies were essentially equal in males and females. The smaller fat bodies of hatchlings at emergence as juveniles indicate that fat bodies are used during hibernation.

Home Range

According to Turner (1971), home range has usually been studied simply because it existed. He suggested that home range should instead be studied in order to solve problems, and he referred to the studies of McNab (1963) and Schoener (1968) and their comparisons of the size of the home range to energy requirements. White (1964) suggested that there is an inverse relationship of density to home range size. Home range size is also useful in studies of density per unit of area and in lizard spacing within a given area. Milstead (1972) stated that home range is important in relation to social behavior and is probably not inherited as display patterns but is environmentally determined by factors such as food and the genetics of the individual. In future studies, telemetry should be explored as a possible method of home range measurement for a three-dimensional area where lizards occupy trees, boulders, etc. Several studies have also considered the subject of home range and territoriality in lizards (Stebbins, 1944; Jennrich and Turner, 1969; Jorgensen and Tanner, 1963; Milstead, 1961 and 1970; Tinkle, 1967a; and Tanner and Hopkin, 1972). However, the subject is still open for further study.

Adult males have a center of activity within their home range, where they are found more often than in other parts of their territory. From late April through June a male is aggressive toward other males found in his home range, especially if the center of activity is approached. This was substantiated by observations of fighting between males and subsequent chasing of the intruder from the home range by the resident male. Fighting did not occur in every encounter. Though there was some overlap in the home ranges of adults, males would not tolerate juveniles of either sex. Female adults could come and go at will, with males performing their display behavior, especially during April and May. Females did not defend their home ranges or centers of activity as vigorously as males. The center of activity appeared to be the most familiar portion of the home range since resident lizards driven away from it tried to return. Stebbins (1944) and Tanner and Hopkin (1972) also reported that there were few encounters among S. o. longipes in southern Nevada. It may be that spacing of lizards (density) in an area can have a profound effect on the
number of encounters that actually take place. The spacing would also be a reflection of the number of lizards an area could support, which would be controlled to a great extent by environmental factors. Therefore, the number of encounters would fluctuate directly with increased density and consequent reduction in size of home range and center of activity (Stebbins, 1944). The density of S. gracilis in California was about 10 per hectare compared to 39 per hectare for adult S. g. graciosus in Utah, which would explain the higher number of encounters in Utah lizards.

The average size of the home ranges of Sceloporus g. graciosus increased as they grew in size from hatchlings to adults, with adult males averaging a larger territory than females. However, overlap in size did exist. Sceloporus olivaceus in Texas showed an overlap in home range with males having larger areas than females (Blair, 1960). Utah gracioso showed a fixity in remaining in the area they established as adults and, to a lesser extent, as juveniles. Stebbins (1944), Blair (1960), and Tanner and Hopkin (1972) noticed similar behavior in S. g. gracilis, S. olivaceus, and S. o. longipes. S. g. graciosus moved from or remained in the area set up while a hatchling, juvenile, or even early in their first adult year (especially males). One reason for these changes may be that hatchlings set up areas in August and September when adult males and juveniles are less aggressive and most have retired for the season. When hatchlings emerge as juveniles they may be within the home range of an adult and be removed. This may happen again to small adult males in their first year. The changes are all by force but this does not rule out passive movement to another area in search of better habitat or food (Stebbins, 1944).

Homing was another aspect of movement in S. g. graciosus observed in all age groups. In adult females, homing consisted of extended forays to lay eggs and then return to the home range. Blair (1960) and Tanner and Hopkin (1972) noticed this in S. olivaceus and S. o. longipes. Mayhew (1963) noted homing in S. orcutti in which animals displaced by the investigator were observed returning to their original home range. Extended forays by S. g. gracioso males and a subsequent return to the original home range occurred after the breeding season and may be typical wandering for adult males. A juvenile, in at least one case of homing, moved from the area of first capture to another area, was captured four times in 17 days, and then moved back within 12.5 m of the original capture. Other juveniles were noted moving away from their home ranges an average distance of 76.6 m. It is not known if these juveniles returned to their original home ranges.

Growth

Growth in S. gracioso has been investigated by Stebbins (1944) and Mueller and Moore (1969). Growth studies of other species of Sceloporus have been done by Fitch (1940), Crenshaw (1955), Mayhew (1963), Davis (1967), and Tanner and Hopkin (1972). Sceloporus g. gracioso in Utah County exhibits growth patterns similar to those for other species; however, there are some differences. From March through most of July only two age groups are present, juveniles and adults. In August, when hatchlings appear, there are three age groups for a short time. After the first two weeks in September only juveniles and hatchlings are abroad, and by the end of September there are only hatchlings.

The presence of yolk in the gut is of considerable importance to the survival of S. g. gracioso hatchlings immediately after hatching. Our data indicate that hatchlings may survive longer than a week without food. Although prey is recognizable soon after hatching, feeding success is low in laboratory hatchlings. Those recently hatched in the field usually have empty stomachs. The adaptive importance of yolk in the gut is in sustaining the hatching long enough to become successful in finding food.

Size of hatchlings at the time of hatching (24.8 mm SVL for males and 25.3 for females) compares well with the sizes reported by Stebbins (1944), Mueller and Moore (1969), and Tinkle (1973). The average size of recent hatchlings of S. g. gracioso is greater than that reported for S. o. longipes by Tanner and Hopkin (1972) and indicates that size of adults of a species does not determine the size of hatchlings.

Hatchling growth rates are equal in the sexes up to the time of hibernation. This is in contrast to growth rates reported by Davis (1967) and Blair (1960), who stated that males grew faster than females in S. occidentalis and S. olivaceus. Blair stated that growth stopped during hibernation, while Davis believed it continued and at an increased rate in males. In S. g. gracioso growth is negligible during hibernation. Stebbins (1944) found the same for S. g. gracilis. A possible explanation for the growth during hibernation reported by Davis (1967) is the warm southern location; however, Blair's (1960) populations were also further south than S. g. gracioso.
Hatchlings in 1970 compared to those of 1971 indicated a significant factor in growth dynamics (Fig. 20, 21, and 22). These data indicate that even though growth rates were the same, the 1971 hatchlings were larger by the time of hibernation. Thus, longer periods of growth have a significant effect on the biomass of the hatching population and juveniles the following year. This may also carry over into the average size of females in their first reproductive year, thereby affecting clutch size and, ultimately, reproductive potential and density of the population. Other factors, such as availability of food and weather variables, would also affect growth during this period.

Hatchlings increased an average of 5.4 mm SVL (20.64 percent) in 1970 before hibernation and 7.22 mm (22.60 percent) in 1971. Mueller and Moore (1969) found that Yellowstone populations of *graciosus* grew an average of 5 mm, which is comparable with 1970 populations from Utah County.

Juveniles grew at a faster rate than other age classes (Fig. 20, 21, and 22). Tanner and Hopkins (1972) stated that *S. o. longipes* averaged 65 to 65 mm SVL in its juvenile year, slightly less than its size at sexual maturity (70 mm SVL) and suggesting that some individuals grow an additional year before reaching sexual maturity. The majority of *graciosus* juveniles in central Utah reached adult size in all years studied and required no additional growth to reach sexual maturity in the spring after the second hibernation.

Juveniles reached adult size at different times in all years studied. When growing seasons were equal in length, the variations in size at emergence were seemingly the result of food availability and weather conditions, both significant factors affecting growth. These factors apparently account for the difference in size between 1970 and 1971 juveniles. A comparison of 1972 juveniles with those of 1970 and 1971 indicates that the above factors were involved; however, an additional growing period of fourteen days resulting from an early spring appears to be an important factor in their larger size.

Davis (1967) stated that *S. occidentalis* juveniles became difficult to distinguish from adults by August. In central Utah populations of *graciosus* this was true of late August juveniles in 1970, late July juveniles in 1971, and second-week-of-July juveniles in 1972.

Adult *S. graciosus* showed sexual size dimorphism that has been found in species of *Sceloporus* such as *S. olivaceus* (Blair, 1960), *S. occidentalis* (Davis, 1967, and Tanner and Hopkins, 1972), and other subspecies (*S. g. gracilis*, Stebbins, 1944). Adult female *S. g. graciosus* were significantly larger than males. This is in contrast to *S. occidentalis* but comparable with *S. g. gracilis* and *S. olivaceus* studied by Stebbins (1944) at Mount Lassen Volcanic National Park, Mueller and Moore (1969) in Yellowstone National Park, and Blair (1960) in Texas. Utah County populations attained an average size significantly larger (70 mm SVL maximum) than those reported for the Mt. Lassen (57.5) or Yellowstone (56.0) populations. The larger size for central Utah populations may be explained by the longer growing season.

Females and males had approximately equal growth rates for the first 13 months. The decline in the growth rate of males at the end of their juvenile year was greater than that of females. Blair (1960) indicated that *S. olivaceus* showed sexual dimorphism as adults. He suggested that increased size in females was an adaptation to allow females to produce a larger number of eggs. This is a plausible explanation and may be operative in *S. g. gracilis* (Fig. 21 and 22); it does not appear to be the case in *S. occidentalis*, where females are equal to or smaller than males (Tanner and Hopkins, 1972). Increased size of older males may be an advantage in maintaining home ranges in strategic areas and, since they are promiscuous, may bring more success in mating. In 1973 Tinkle conducted a study of *graciosus* in southern Utah approximately 300 miles south of the study plot. The density for his plot was 205 juveniles and adults per ha, with a biomass of 980 g. Central Utah populations had a density of 66 juveniles and adults per ha and a biomass of 409 g (August). These differences indicate that different habitats have different carrying capacities. In addition, though Tinkle's densities were three times greater than those of the central Utah study plot, his biomass was just over two times. The apparent reason for the large biomass of Central Utah lizards in proportion to density is their larger average size as adults (635 g, males and 7.20 g, females) and proportionately larger juveniles.

Sex ratios of *S. g. gracilis* were statistically similar even though females were approximately 8 percent more abundant in resident juvenile and adult populations of the study plot. This is in contrast to findings of Mueller and Moore (1969), who found *S. g. gracilis* in Yellowstone National Park to have an equal sex ratio in all age classes except adults, where it was in favor of females (64 percent). From this it appears that greater mortality in males takes place in the first reproductive year. Blair (1960).
however, reported that the uneven sex ratio in S. olivaceus was caused by a differential mor-
tality that began from an equal sex ratio at hatching. He further stated that the greater
number of females may be an adaptation for
greater production of eggs. He continued by
stating that this was explained by differential
mortality in males and their promiscuous be-
behavior; therefore, fewer males are needed and
this leaves more energy and area in the environ-
ment to support the more valuable females.
Tinkle (1973) indicated this possibility for
southern Utah populations of graciosus, where
females (adult) were as abundant as those re-
searched by Mueller and Moore in Yellowstone
National Park. Even though the abundance of
females from the juvenile year on in central Utah
is not as great as those mentioned above, the
same principles suggested by Blair may operate
to a lesser degree in central Utah. These addi-
tional factors may be also operative: first, young
adult males are less successful in combat and
are driven to less favorable habitats where mor-
tality rates may be higher; second, males emerge
earlier in the spring and are exposed to preda-
tion longer than females; third, males by their
display behavior are more often exposed to preda-
tion.

It may be that the high number of females
observed by Mueller and Moore (1969) was due
to females migrating into the area to lay eggs
and then leaving, as was noticed by Blair
(1960) and Tanner and Hopkin (1972). In
Utah populations there was also a significant
number of additional females in June and July
on the study plot (Table 5). These were not
part of the resident females occupying the study
plot throughout the year.

Rand (1972) suggested that female iguanas
select open sandy areas to lay their eggs, where
the sun's rays will provide maximum heat to in-
sure fastest development and the most success-
ful incubation. In central Utah, females were
observed migrating to the study plot (from ad-

cjacent areas) which had a south-facing slope
(where most migrants were found) with sandy
soil and open areas. It was also noticed that
there was little migration of females at the time
of oviposition, which may account for the high
number of females noticed by Mueller and
Moore (1969) migrating to the thermal areas to
lay eggs.

Population dynamics in Utah County are
best compared with the study conducted by
Stebbins and Robinson (1946) on S. g. gracilis
at an elevation of 1,829 m in Lassen Volcanic
National Park in Montane forest (Transitional
Boreal). This population was approximately
305 m higher than those in central Utah, at
about 1,524 m in an oak-maple and sagebrush
association primarily in the Transitional Life
Zone. The two populations are compared as fol-
lows: California lizards were smaller in size and
had a longer life span, population replacement
was slower, the growing period was less (150-
160 days vs. 180-190 in Utah), and the average
clutch size was much less (3.3 in California vs.
6.03 in Utah). These differences seem explained
on the basis of the habitats of the two popula-
tions. Stebbins and Robinson (1946) compared
the population of S. g. gracilis with the lowland
S. occidentalis studied by Fitch (1940) and sug-
gested that possible reasons for lower clutch size
and longer life span were fewer predators; a
shorter activity period, which reduced exposure
to predators; and fewer young, leading to a
slower turnover in the population. Though
these factors are connected with a longer life
span and lower clutch size, there are possibly
other factors.

California populations are adapted to the
higher altitude and its abiotic and biotic en-
vironments. This creates a combination of fac-
tors such as shorter growth period, reduction
in size (SVL), and an increase in the life span
compared to Utah. Also, there are fewer days
of exposure to predators and possibly fewer
predators. The reduction in SVL is associated
with reduction in clutch size; therefore, the
only way for the population to remain stable
is to increase the life span and number of re-
productive years. Thus environmental factors
associated with the greater elevation evidently
have reduced the number of predators, the
growth period, and exposure to predation. The
growth reduction may have a fortuitous effect
in that lizards would warm faster, an advantage
at higher altitudes. Mueller and Moore's (1969)
study of S. g. graciosus at 2,316 m in Yellow-
stone National Park lends support to the sug-
gestation that increased altitude reduces indi-
vidual size and consequently clutch size, with
essentially the same values as those of California
populations.

In contrast, Utah populations produce a
clutch almost twice as large and attain an indi-

cidual size 5 to 7 mm SVL larger, which al-

ows for the larger clutches. These differences
appear to be connected to the longer growing
period and greater turnover in the population
(possibly due to greater predation), which is
manifest by the shorter life span; therefore, a
larger clutch size is necessary to maintain the
population at a stable level. It appears from
these comparisons that different populations of
S. graciosus have adapted to different habitats
by modification of their life cycle. Tanner (1972) observed the reverse situation in *Uta stansburiana*, which attains a larger size at higher elevations and also larger clutches but is similar to California populations of *graciosus* in having a longer life span. The effects of elevation and latitude on various habitats occupied by a species have also been discussed by McCoy and Hoddenbach (1966) and Burkholder and Walker (1973) for *Cnemidophorus tigris*.

**Demography**

Lizard demography and reproductive strategies have been studied by Turner, Medica, Lannom, and Hoddenbach (1969); Turner, Hoddenbach, Medica, and Lannom (1970); Tinkle (1967b); Tinkle (1969); Tinkle (1973); and Tinkle, Wilber, and Tilley (1969). Tinkle (1973) reported on the life strategy and demography of *S. g. graciosus* in southern Utah. In central Utah *S. g. graciosus* is a single-brooded, late-maturing subspecies, with a reproductive life span of about four and possibly five years, a mean life expectancy of 30.13 months, and a breeding age of 23.0 months. A comparison of these data with those of Stebbins (1944-1948) and Stebbins and Robison (1946) indicates that Utah populations mature faster (23 vs. 48 months [after Tinkle, 1969]), have a longer mean life span (30.1 vs. 25.5 months [after Tinkle, et al., 1969]), and a larger clutch size (6.03 vs. 3.33). However, California populations apparently have a longer life span, nine years, in contrast to six or seven years in central Utah. According to Tinkle (1973), it would appear from these data that California populations would have difficulty maintaining themselves.

Tinkle (1973), reporting on a southern Utah population of *graciosus*, had the following breakdown of demographic statistics: breeding age 21 to 22 months; mean life expectancy of approximately 3.0 years or 36 months; clutch size of 4.2, with two clutches produced in one season; and a life span identical to that reported by Stebbins (1948) of nine years, in fact using Stebbins’s ages rather than what may be the actual longevity in southern Utah. These statistics differ considerably from those of central Utah populations. The only similarity in the two populations is the age of breeding (about 22 months). Contrasting points are mean life expectancy, clutch size, number of clutches per year, and longevity of the animals. These contrasting features are reduced in magnitude when we consider the R-values for Central Utah *graciosus* and .975 for those in southern Utah which are approaching unity, suggesting that both populations are at approximate stability and possibly at the carrying capacity of their separate habitats. A noteworthy point is that central Utah *graciosus* achieve near unity with one large clutch and southern forms with two small clutches. In addition, the R-values for central Utah populations are conservative, since only four reproductive years were used and not five. A possible explanation for the different demographic statistics and/or method of achieving stability in the two populations is yearly survivorship. Survivorship of hatchlings to juveniles (yearlings) for the two populations is about the same at 23 percent (mortality being caused by overwintering). However, the big difference occurs in juveniles to first-year adults: 90 percent in central Utah and 60 percent in southern Utah. The 20 percent difference is perhaps sufficient to compensate for higher total egg production and longevity of southern Utah *graciosus*. The lower survivorship of southern Utah populations (yearlings to adults) may be due to higher predation of southern populations as suggested by Blair (1960).

In conclusion, we agree with Tinkle (1973) that *S. g. graciosus* is a late-maturing species. Otherwise, our data are at variance either in detail or in such major aspects as SVL, clutch size, longevity, and density. In view of the differences noted in the four studies (Stebbins and Robinson, 1946; Mueller and Moore, 1969; and Tinkle, 1973), it is obvious that *graciosus* is a species with considerable adaptive flexibility.

**LITERATURE CITED**


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