

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 158

**Populations in a Fluctuating Environment:
The Comparative Population Ecology of the
Iguanid Lizards *Sceloporus merriami* and
*Urosaurus ornatus***

by
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Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
April 30, 1981

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WILLIAM D. HAMILTON

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INTRODUCTION

Following the pioneering efforts of Blair (1960) and Tinkle (1967), numerous investigators have documented variation in life histories, population dynamics, and demography both between lizard species (Ballinger, 1973; Smith, 1977; Tinkle, Wilbur, and Tilley, 1970; Turner et al., 1970; Vinegar, 1972; and others) and among populations of a species (Ballinger, 1977; Parker and Pianka, 1975; Tinkle, 1967; Tinkle and Ballinger, 1972; VanDevender, 1975; and others). Several workers have demonstrated significant variation in individual growth rates and/or life histories which is related to proximal variation in food resource availability (Ballinger, 1977; Dunham, 1978a, b; Martin, 1973, 1977; Schoener and Schoener, 1978). Smith (1977) and Vinegar (1972) showed that age-specific survivorship, age-specific fecundity, body size, and individual growth rates varied seasonally and among years in populations of the striped plateau lizard (*Sceloporus virgatus*) from southeastern Arizona. Martin (1973, 1977) reported differences in reproductive success and body size in a population of the tree lizard (*Urosaurus ornatus*) from central Texas which were correlated with the occurrence of drought conditions. Ballinger (1977) has shown that during years of drought and, hence, lowered food abundance, size-specific fecundity and clutch frequency were reduced in a population of *Urosaurus ornatus* from the Animas mountains of southwestern New Mexico. Smith (1977) demonstrated significant yearly variation in individual growth rates which was correlated with drought conditions in a population of *Urosaurus ornatus* from the Chiricahua Mountains of southeastern Arizona. I showed that temporal variation in the amount of precipitation results in predictable variation in the abundance of arthropod prey available to the canyon lizard (*Sceloporus merriami*) with concomitant variation in individual growth rates (Dunham, 1978a). The work of several investigators suggests that different populations of the same species may differ greatly in the degree to which they are subject to predation or in the degree to which they are affected by temporal variation in resources (Andrews and Rand, 1974; Ballinger, 1979; Parker and Pianka, 1975; Tinkle and Ballinger, 1972; and others). This review, while not exhaustive, suggests that lizard populations in arid and semi-arid ecosystems typically exhibit considerable variation in life history traits such as age-specific survival, individual growth rates, and clutch fre-

quency in response to temporal fluctuation in food resource abundance or other environmental variables that are affected by temporal variation in the amount of precipitation. The studies cited here further suggest that lizard communities differ in the extent to which their component species are limited by predation or resource abundance, and therefore, in the degree to which interspecific competition is important in lizard community structure. Elsewhere (Dunham, 1978b, 1980), I reported the results of a long-term experimental study of interspecific competition in a simple guild consisting of two abundant species of iguanid lizards, the canyon lizard, *Sceloporus merriami*, and the tree lizard, *Urosaurus ornatus*, at a location of ecological microsympatry in southwestern Texas. In the present paper, I compare the population ecology and demography of the populations of *Sceloporus merriami* and *Urosaurus ornatus* occurring in the Grapevine Hills of Big Bend National Park, Texas. I also report the results of a study of the effects of variation in food resource abundance on individual foraging success, age-specific survival, age-specific fecundity, clutch frequency, prehibernation lipid storage, and individual growth rates.

Sceloporus merriami is a small iguanid lizard whose geographic distribution includes only southwestern Texas and parts of the adjacent Mexican states of Coahuila and Chihuahua (Olson, 1973). It is saxicolous throughout its range and is found at elevations from about 350 to over 1700 m. Prior to this study the biology of the canyon lizard received little attention. On the basis of a single collection, Chaney and Gordon (1954) provided data on clutch size, body size at sexual maturity, and qualitative data on food habits. Carpenter (1961) described some of the behavioral patterns associated with social interaction. Milstead (1961) hypothesized a competitive interaction with *U. ornatus* and provided a detailed description of territorial and mating behavior. Olson (1973) provided a taxonomic review and an analysis of geographic variation based primarily on scalation.

The tree lizard has been more intensively studied. It ranges from central Texas and the southern Rio Grande Valley, west as far as southeastern California, south in western Mexico to central Sinaloa, and north to Utah, Colorado, and southwestern Wyoming (Stebbins, 1966; Conant, 1975). *Urosaurus ornatus* is arboreal, semiarboreal, or saxicolous throughout its range. A number of workers have discussed the reproductive biology of *U. ornatus* including Asplund and Lowe (1964), Ballinger (1977), Martin (1973, 1977), Michel (1976), Smith (1977), and Van Loben Sels (1976). Ballinger (1976, 1977) and Smith (1977) have provided valuable demographic analyses for populations in southwestern New Mexico and southeastern Arizona, respectively. Asplund (1964) documented seasonal variation in the diet of a riparian population of tree lizards. Hibernacula have been described by Worthington and Sabbath (1966) and Vitt (1974). Data on the behavior of *U. ornatus* were provided by Carpenter and Grubitz (1960, 1961) and by Purdue and Carpenter (1972). Milstead (1970) compared the territorial and reproductive behavior of *U. ornatus* and *S. merriami*.

METHODS

THE STUDY SYSTEM AND LIZARD COMMUNITY.—The study area is located at an elevation of approximately 1036 m in the Grapevine Hills of Big Bend National Park, Texas within the Lechuguilla-Creosote-Cactus Association of the Chihuahuan Desert (Wauer, 1971). Numerically dominant perennial plant species include three-awn grass (*Aristida* spp.), mariola (*Parthenium incanum*), Texas persimmon (*Diospyros texana*), lechuguilla (*Agave lechuguilla*), ocotillo (*Fouquieria splendens*), prickly pear (*Opuntia engelmannii*), sotol (*Dasyliirion leiophyllum*), Torrey yucca (*Yucca torreyi*), catclaw mimosa (*Mimosa biuncifera*), skeleton-leaf goldeneye (*Viguiera stenoloba*), creosote (*Larrea tridentata*), mesquite (*Prosopis glandulosa*), and shrub acacias (*Acacia* spp.). Descriptions and characteristics of Big Bend vegetation have been provided by Muller (1937), Denyes (1956), and Wauer (1971).

The lizard community in the Grapevine Hills includes at least 12 species. These are the tree lizard (*Urosaurus ornatus*), the canyon lizard (*Sceloporus merriami*), the marbled whiptail (*Cnemidophorus tigris*), the rusty-rumped whiptail (*Cnemidophorus scalaris*), the greater earless lizard (*Cophosaurus texanus*), the side-blotched lizard (*Uta stansburiana*), the twin-spotted spiny lizard (*Sceloporus magister*), the southern prairie lizard (*Sceloporus undulatus*), the Great Plains skink (*Eumeces obsoletus*), the collared lizard (*Crotaphytus collaris*), the Texas horned lizard (*Phrynosoma cornutum*), and the Texas banded gecko (*Coleonyx brevis*).

Potential predators on populations of *Sceloporus merriami* and *Urosaurus ornatus* in the Grapevine Hills are common and include: the central Texas whipsnake (*Masticophis taeniatus*), the western coachwhip (*Masticophis flagellum*), the Big Bend patch-nosed snake (*Salvadora grahamiae*), the black-tailed rattlesnake (*Crotalus molossus*), the mottled rock rattlesnake (*Crotalus lepidus*), the collared lizard (*Crotaphytus collaris*), the Great Plains skink (*Eumeces obsoletus*), the Road Runner (*Geococcyx californianus*), the Loggerhead Shrike (*Lanius ludovicianus*), and the Cactus Wren (*Campylorhynchus brunneicapillus*). The whiptails *Cnemidophorus tigris* and *C. scalaris* are potential predators on the eggs of *S. merriami* and *U. ornatus*. Of these, only *M. taeniatus*, *S. deserticola*, *C. molossus*, *C. lepidus*, *E. obsoletus*, *C. scalaris* and *C. brunneicapillus* were common on the study area and probably represent the important predators on the canyon lizard and tree lizard populations studied here.

During the course of this study daily precipitation data were available from a U.S. weather station located at Panther Junction, Big Bend National Park at an elevation of 1140 m, 9.3 km SSE of the study area. The weather data for the study area were summarized by Dunham (1978a).

THE STUDY POPULATION.—In May 1974, two comparable sites within the study area described above were selected as control plots for the experimental study of competition between *S. merriami* and *U. ornatus* described elsewhere (Dunham 1978b, 1980). These were designated plots I (0.53 ha) and IV (0.83 ha) in that study and I will retain that designation here. These plots were chosen because they were inhabited by dense populations of *S. merriami*

and *U. ornatus* and because they were separated from other such sites by habitat unsuitable for these lizards. Unless otherwise indicated, all of the data presented here were taken from individuals inhabiting these two study plots.

DEMOGRAPHY.—Populations of *S. merriami* and *U. ornatus* inhabiting the study plots described above were censused, at least monthly, from May through September of 1975, 1976 and 1977. In 1974, these plots were censused from May–August. The study plots were sampled twice in June, July, and August of each year. On each sampling date my assistants and I searched the area systematically and attempted to capture all residents using a noose attached to a fishing pole. Each new lizard was sexed, given a unique identifying number and corresponding toe clip (Tinkle, 1967), given a unique paint mark, weighed to the nearest 0.1 g using a Pesola® spring scale, and the snout-to-vent length, SVL, measured to the nearest 0.5 mm using a clear plastic ruler. Animals of all ages could be accurately sexed because the males of both species have enlarged postanal scales and the adults of both species exhibit sexual dimorphism in coloration. At each capture, the reproductive condition of females was determined by palpation (Tinkle, 1967). At each succeeding capture, the animal was identified, repainted if it had shed its paint mark, and all of the above data recorded. I took all measurements to minimize error due to differences among observers. Lizards were released at the point where they were first seen.

The lizard density on each plot was estimated from the total number of animals actually registered on each plot and from the small-sample Lincoln–Peterson estimate (Seber, 1973; Chapman, 1951). Estimates for early June were used to compare the densities on each plot for each year of the study because these are the sampling dates closest to the onset of oviposition.

There are two types of bias in recapture estimates of population density (Seber, 1973). Bias arises from capture heterogeneity or consistent differences in catchability among individuals, and from contagion, in which the conditional probability that an animal will be captured given that it is at risk $P(C|R)$ varies as a function of capture history. Although clearly present, contagion was not analyzed quantitatively for either species. Individuals became more difficult to noose with increasing capture frequency. Also, it was obvious that in spite of attempts to search each area systematically, locations where lizards had been recently captured were examined more carefully than locations where lizards had not been recently caught. The effect of this is that individuals which had prominent perches or which had been recently or frequently captured were probably more likely to be captured during a given sampling effort than would otherwise be the case. These two sources of contagion should partially counteract one another, and the actual bias introduced due to contagion is likely to be a complex function of recapture history.

AGING.—Individuals were aged according to their size (SVL) at first capture and their initial growth history. Animals marked shortly after hatching were

easily separated by their small size, and frequently by the presence of a yolk scar, from older animals. These animals were marked and could be aged with certainty at each succeeding recapture. Most animals were first captured in May or June of the year following hatching and were aged according to their size at that time. The frequency distributions of body size (Fig. 1) were polymodal at that time, and the lengths of animals of known age indicate that in each case, the smaller individuals were in their first year following hatching (the yearling age class) and the larger animals represented a mixture of older age classes. Some animals, particularly *U. ornatus*, were intermediate in size at first capture and could not be aged with certainty. These individuals were assigned to the most likely age class given their size, subsequent growth history, and the survivorship schedules characterizing the population to which they belonged.

FECUNDITY AND REPRODUCTIVE DATA.—Samples for reproductive data were taken from similar habitat within 2 km of the study plots. Reproductive samples were taken at least monthly from May through September of 1975, 1976 and 1977 and every two weeks during May—August of 1974. In 1976 and 1977 animals were frozen for quantitative lipid determination (see section on storage lipids). In all cases autopsied animals were weighed to the nearest 0.1 g and the SVL measured to the nearest 0.5 mm. In females, numbers of yolked follicles (ovarian eggs), oviductal eggs and corpora lutea were recorded. The greatest length (a) and width (b) of each oviductal egg were measured to the nearest 0.1 mm with vernier calipers. The volume of each egg was estimated from the equation for the volume of a prolate spheroid (Selby, 1965):

$$V = 4/3 \pi (a/2) (b/2)^2.$$

Total clutch volume was estimated as the sum of the volume estimates of the individual eggs. In 1976 and 1977, oviductal eggs were removed and weighed to the nearest 0.1 mg. Each egg was then dried to constant weight on a freeze drying apparatus and reweighed. The percent water content of each egg was determined as the ratio of dry weight to wet weight.

The simultaneous occurrence of oviductal eggs with either corpora lutea or yolked follicles was viewed as evidence for the production of more than one clutch per season. Linear regression models relating clutch size (number of eggs per clutch) to SVL were constructed for each species. Clutch size was determined by direct count of oviductal eggs, corpora lutea, or yolked follicles ≥ 4 mm in diameter. This size was chosen because follicular atresia was not observed in follicles of either species after this diameter had been attained. Different regression models were estimated from the reproductive data for each year of the study. Logarithmic transformation of the variables was necessary to obtain homogeneity of the residuals as assumed in linear regression analysis (Draper and Smith, 1966). These models were used to predict the total number of eggs produced on each study area by females of each species in each year of the study from the body size distributions of the females at the time each clutch was produced. Some reproductive data were

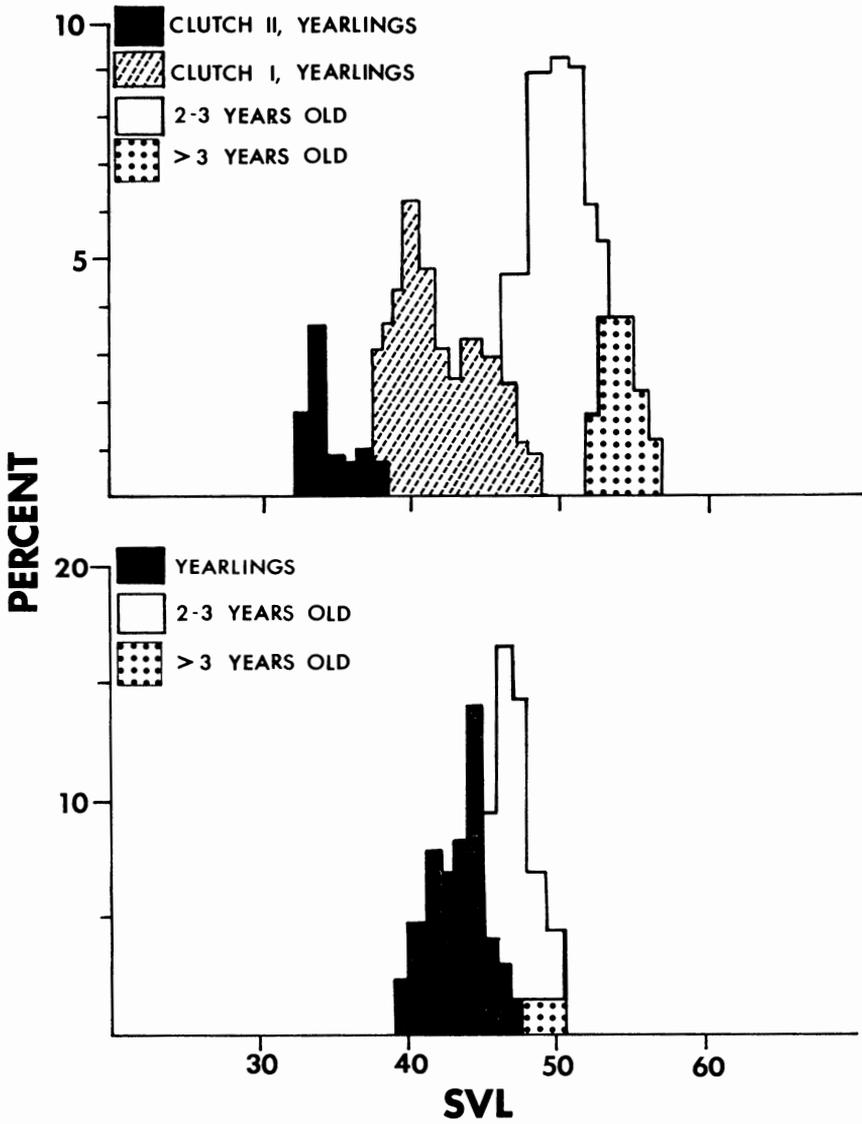


Fig. 1 Size (SVL) frequently distribution of known age female *S. merriami* (top) and *U. ornatus* in late May - early June of 1976.

obtained from individuals captured on the study plots. The reproductive condition of each female was noted at each capture. Females which had recently oviposited frequently could be recognized because they had mud caked on their feet and chin and had lost weight approximately equal to the weight of a clutch (0.5 – 1.0 g) and/or because they had changed from a gravid to a non-gravid condition. Data from the periodic recapture of individually marked females were used to estimate clutch frequency (number of clutches per season) as well as the size and age at first reproduction.

In males, the length of the left testis was measured to the nearest 0.1 mm, and the epididymis and vas deferens were examined for the presence of the milky white seminal fluid normally indicative of the presence of sperm. The presence during the breeding season (May – mid-August) of enlarged testes with visible seminiferous tubules and with seminal fluid in the epididymides and vas deferens was taken to indicate sexual maturity.

STORAGE LIPIDS.—The fat bodies (*corpora adiposa*) of both sexes were removed and weighed to the nearest 0.01 g in 1974 and 1975. In 1976 and 1977 the animals taken in the reproductive samples were frozen in the field and transported back to the laboratory for quantitative lipid determination. The fat bodies and liver of each animal were removed and weighed to the nearest 0.1 mg. The stomach and gut contents were removed for analysis. The fat bodies, liver, and remaining carcass of each animal were then dried to constant weight on a freeze drying apparatus and weighed. The carcass was then homogenized by grinding in a Wiley mill. The lipids were then separately extracted in excess chloroform from the liver, fat bodies, and a sample of the homogenized carcass. The dissolved lipids and solvent were then separated under a vacuum in a rotary evaporator, and the dry weight of lipid in each compartment determined to the nearest 0.1 mg. Only data taken from animals in the prehibernation sample (late September – early October) are presented here. The total prehibernation lipid storage of an animal was taken to be the sum of the dry weights of chloroform extractable lipid in the fat bodies, liver, and carcass. Linear regression models relating SVL and wet body weight and SVL and total prehibernation lipid storage were computed for each species using the logarithmically transformed variables. Separate models were computed for each sex and year. These models were then compared using the analysis of covariance (ANCOVA).

SURVIVAL.—For animals 1 year old or older, annual survivorship was estimated as the ratio of the group of marked animals known to be alive in early June of one year to the total number of marked animals known to be alive in early June of the previous year. survivorship from age 0 to age 1 year was estimated as the ratio of the small-sample Lincoln–Peterson estimate (Seber, 1973) of the number of yearling animals alive on a particular plot in June of a given year to the estimated number of eggs produced by the sexually mature females living on that plot when clutches were produced the previous year. Survival from hatching to June of the following year was estimated by the ratio of the number of marked hatchlings known to survive

until June of a given year to the number marked the previous year. Survivorship was estimated separately for each age class and sex of each species on each study plot in each year of the study.

INDIVIDUAL GROWTH.—The recapture data collected during this study were used to estimate the free parameters, asymptotic body size (A) and the characteristic growth rate (r), of the logistic-by-weight growth model utilizing a non-linear least squares regression procedure. Details of this growth analysis are presented by Schoener and Schoener (1978) and Dunham (1978a, b). Elsewhere, I showed that the logistic-by-weight growth model provided a better fit to the recapture data for these two species than did either the Von Bertalanffy or the logistic-by-length models (Dunham, 1978a, b). In each case, the logistic-by-weight model resulted in a lower residual error mean square when fit to the recapture data. Only recapture intervals longer than 20 days were used in parameter estimation in order to minimize the effects of measurement error. Snout-to-vent length was used as the measure of body size in all models. The other possible measure (body weight) varies as a function of reproductive condition (especially in females) and recent nutritional history to a much greater extent than does SVL. Consequently, SVL has a lower error variance associated with its measurement and is a better measure of body size. The differential equations used for the logistic-by-weight model describe the change in length when weight is changing logistically so the model can be fit to recapture data which use length as a measure of body size (Dunham, 1978a). Separate models were fit to the recapture data from *U. ornatus* and *S. merriami* from each of the study plots. In the absence of significant differences between plots, models were fit to the combined data from the two plots. Models were estimated from the data for each year of the study.

Non-linear least squares regression models allow several types of confidence intervals to be constructed around the parameters estimated for each growth model because asymptotic standard deviations are computed for each parameter estimated (Marquardt, 1964; Schoener and Schoener, 1978; Dunham, 1978a). Following Marquardt (1964), I constructed 95% “support plane” confidence intervals about the parameters estimated in each model. The “support plane” confidence interval is the maximum symmetrical confidence interval about a given parameter, regardless of the value of the other parameter in the model. In contrasting different growth models, parameter estimates were considered different if the 95% “support plane” confidence intervals did not overlap. This is an extremely conservative test.

FOOD AVAILABILITY.—I used two methods to estimate the abundance of potential prey for *S. merriami* and *U. ornatus*. In 1975, 1976, and 1977 squares of 3 inch masking tape (58.06 cm²) were affixed to rock surfaces where these lizards normally fed. The exposed surface of each square was then coated with the insect trapping adhesive tanglefoot[™]. These “sticky traps” were used regularly from May through October of these years to sample arthropod abundance on the study plots. On each sampling date, at least 12 sticky traps were placed on each plot and the exact time each trap was

set recorded. Traps were left in place at least 24 hr, and at each reading, the time and number of arthropods trapped recorded. These data were converted to capture rates and expressed as arthropods trapped trap⁻¹ hr⁻¹. Similar methods have been used by Ballinger (1977) and Simon (1975). The null hypothesis, that there were no differences in arthropod abundance as measured by these traps on comparable sampling dates in 1975, 1976, and 1977 was tested using Mann-Whitney U tests.

In 1976 and 1977 an additional arthropod sampling technique was used to provide data for comparison with the results of sticky trap sampling. A D-Vac[™] vacuum arthropod sampling device was used to sample the arthropod abundance on each plot. During each sampling period, open rock surfaces where *S. merriami* and *U. ornatus* normally foraged were sampled for periods of about 2 min. duration. The exact duration of each sample was determined with a stopwatch. On each sampling date, two samples were taken on each control site between 0930 and 1145, and the total number of arthropods captured and duration of the sample recorded. These data were converted to a capture rate (arthropods captured per minute).

INDIVIDUAL FORAGING SUCCESS.—I employed three measures of individual foraging success in these lizards. The first method consisted of weighing the stomach contents of the adult male *S. merriami* and *U. ornatus* taken for reproductive data. Data from female lizards were not used because gravid females, especially those with large yolked follicles or oviductal eggs, eat very little compared to nongravid females or males, and I timed the reproductive samples to maximize the proportion of gravid females captured. As a result, sample sizes of non-gravid females were often too low for comparison and there was no way to control for the confounding effect of having both gravid and non-gravid females in the samples. I present here data from animals taken in 1976 and 1977.

The second method of estimating individual foraging success consisted of direct field observation foraging males of both species. My assistants and I observed individually marked lizards on the study sites in 1976 and 1977. These observations were carried out between 0800 and 1100 CDT, and only data from actively foraging males were used in the analysis. The duration of observation of each individual was timed with a stopwatch, and the number of feeding strikes made by the animal counted. These data were converted into a feeding rate. In order to have observation of an adequate number of lizards, I lumped the data from 1976 into samples from 3 two-week intervals, late June, early August, and late August.

The final method of estimating individual foraging success involved the quantification of prehibernation lipid storage in males and females of both species in a wet year (1976) and dry year (1977). Using the chloroform extraction technique described above, I extracted and quantified the total body lipids from animals collected in late September and early October of 1976 and 1977 and used this as an estimate of an individual's foraging success in the preceeding active season (April–October).

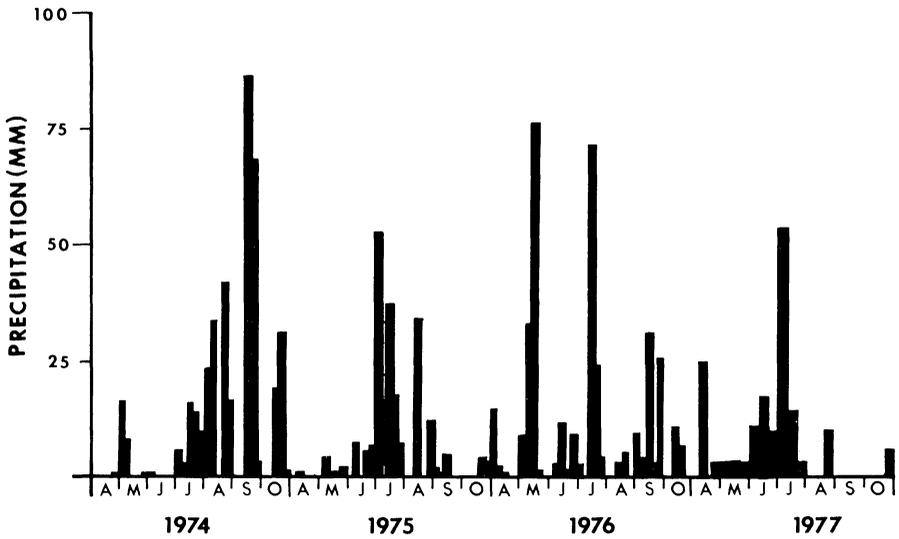


Fig. 2 Active season precipitation during this study (1974 - 1977).

In all statistical procedures used in this analysis, I employed parametric tests of hypotheses when the data did not seriously violate the assumptions of those tests. I used analogous nonparametric procedures (Conover, 1971) when the assumptions of appropriate parametric procedures could not be met. In all statistical tests, the null hypothesis was rejected if the attained level of significance was ≤ 0.05 .

RESULTS

RAINFALL AND PREY ABUNDANCE.—The amount and distribution of precipitation differed greatly in the four years of this study (Fig. 2). The total annual precipitation was 48.0 cm in 1974, 21.4 cm in 1975, 44.7 cm in 1976, and 17.2 cm in 1977. The total active season (April – October) precipitation was 40.9 cm in 1974, 18.1 cm in 1975, 37.2 cm in 1976, and 15.5 cm in 1977. The mean annual precipitation based on 20 yr continuous data is 32.7 ± 4.2 (95% CI) cm: the mean active season precipitation for the same period is 26.8 ± 4.2 cm. Clearly 1975 and 1977 were much drier than 1974 and 1976, and both years were significantly drier than the long-term average for both annual and active season precipitation; 1977 was the driest year since the establishment of the U.S. weather station at Panther Junction (1956).

Arthropod abundance estimated from sticky traps suggests that saxicolous insectivores such as *S. merriami* and *U. ornatus* had significantly more prey available in 1976 than in either 1975 or 1977 (Fig. 3). The mean estimate for every sampling date in 1976 was greater than that for the corresponding sampling date in either 1975 or 1977. Mann–Whitney U

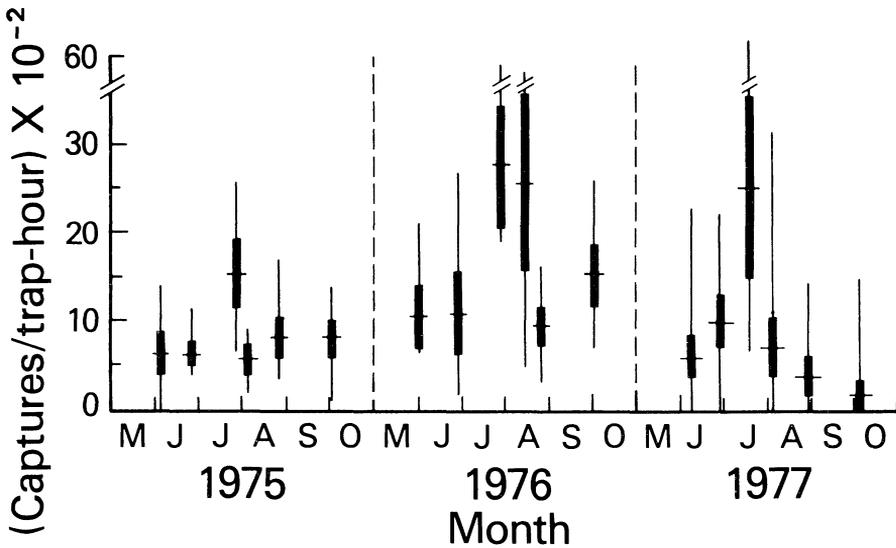


Fig. 3 Tanglefoot[®] trap estimates of arthropod abundance on the study plots during 1975-1977. Vertical line is the range, horizontal line is the mean, and the vertical bar is the 75% error bound (2 SE).

pairwise comparisons revealed that in all but 2 cases the differences were statistically significant ($p < 0.05$). The 1976 estimate for late June was greater than that for the same period in 1975 but the difference was not statistically significant ($p = 0.13$). The same was true for the comparison of the late August estimate for 1976 with that for 1975 ($p = 0.08$). Pairwise Mann-Whitney U comparisons of the sticky trap estimates for comparable sampling dates revealed that arthropod abundance was significantly greater in 1976 than in either 1975 ($U = 31, 0.01 \leq p \leq 0.025$) or 1977 ($U = 33, 0.005 \leq p \leq 0.01$) but that the abundance estimates for 1975 and 1977 did not differ significantly ($U = 15, p > 0.10$).

In the years for which data are adequate (1976 and 1977), the highest serial correlation ($r = 0.646, p \leq 0.05$) between the D-Vac[™] estimate of arthropod abundance and precipitation was with the amount of precipitation in the preceding two week time interval. The two methods of estimating prey abundance were concordant in their estimates; there was a highly significant Spearman rank correlation ($r_s = 0.83, 0.01 \leq p \leq 0.003$) between the sticky trap and D-Vac[™] estimates of arthropod abundance for 1976 and 1977. Neither method provides an unbiased quantitative estimate for the abundance of food resources available to *S. merriami* and *U. ornatus* at any given time. Ants, for example, are not well sampled by sticky traps. Both methods do, however, sample the same array of prey types and sizes as is found in the stomachs of these lizards and thus presumably provide satisfactory indices of the relative abundance of prey available at different times.

TABLE 1
COMPARISON OF THE CONDITIONAL PROBABILITY P(C|R) OF CAPTURE AT LEAST ONCE DURING AN ACTIVE SEASON, GIVEN THAT AN ANIMAL IS KNOWN TO BE AT RISK. SEE TEXT FOR DETAILS.

Species	Sex	# Surviving 3 Years	# Captured in 2nd Year	P(C R)
<i>Sceloporus merriami</i>	Male	155	149	0.9613
	Female	84	75	0.8929
<i>Urosaurus ornatus</i>	Male	62	61	0.9839
	Female	34	28	0.8235

TABLE 2
SUMMARY OF χ^2 COMPARISONS OF CONDITIONAL PROBABILITY OF CAPTURE GIVEN THAT AN ANIMAL IS KNOWN TO BE AT RISK (P(C|R)). DATA FROM TABLE 1.

<i>Sceloporus merriami</i> females	4.34 (0.0372)		
<i>Urosaurus ornatus</i> males	0.72 (0.3951)	4.53 (0.0333)	
<i>Urosaurus ornatus</i> females	8.90 (0.0029)	1.05 (0.3055)	8.35 (0.0039)
χ^2 (p)	<i>Sceloporus merriami</i> males	<i>Sceloporus merriami</i> females	<i>Urosaurus ornatus</i> males

POPULATION ESTIMATION.—Analysis of recapture records was used to evaluate the completeness of population enumeration. Records of animals known to have survived in the control populations at least three years were used to estimate the proportion (P(C|R)) of animals that were not captured given that they were known to be at risk. These data are summarized in Table 1 and indicate that males and females of both species differ significantly (Table 2) in catchability. Of 155 male *S. merriami* known to have survived three years, 149 were captured during the second year. If these represent a simple random sample of the population alive during the second year, 96% of the male canyon lizards alive then and previously marked were actually captured at least once during the active season of the second year. In contrast, 75 of 84 (89%) of the female canyon lizards known to have survived three years were captured at least once during the second year. Of 62 male

tree lizards known to have survived three years, 61 (98%) were captured in the second year; only 28 of 34 (82%) of the female tree lizards known to have survived three years were captured during the second year. The observed differences in catchability of male and female canyon lizards ($\chi_1^2 = 4.34$, $p = 0.037$) and tree lizards ($\chi_1^2 = 8.25$, $p = 0.004$) are statistically significant (Table 2). The differences in catchability were obvious in the field. Both species exhibit intraspecific territoriality, and during the breeding season (May through early August) males are active in territorial defense and courtship. As a result, they are quite conspicuous and therefore easily enumerated. Females, on the other hand, are more secretive, especially when ovigerous, and normally do not engage in territorial defense until after the breeding season.

The total number of adults captured and the small sample Lincoln-Peterson estimate of the number of adults residing on each of the study plots in early June of each year of the study are presented in Tables 3 and 4. For those age classes in which too few animals were present to allow calculation of Lincoln-Peterson estimates, the total number of animals actually registered was used as a measure of population size. The two estimates (Fig. 4) are highly correlated in both *S. merriami* ($r = 0.96$; $p \leq 0.001$) and *U. ornatus* ($r = 0.89$; $p \leq 0.001$). Early June densities of adults of each species based on the pooled data from the two study sites are summarized in Fig. 5.

The effects of bias arising from capture heterogeneity or contagion on the estimates of the density of the adult lizard populations on each study plot cannot be judged with certainty. However, because of the high sampling effort and the small proportion of adult lizards which escaped capture when known to be at risk (Table 1), I don't believe the bias to be serious. On the other hand, hatchlings of both species were obviously less catchable than were the adults. Because of the small number of animals caught more than once in the year in which they hatched, quantitative comparison of hatchling catchability between species or with that of adults of the same species was not possible. Therefore, comparison of small sample Lincoln-Peterson estimates of the number of hatchlings emerging on each plot in each year should be viewed with caution.

CHANGES IN POPULATION SIZE.—The adult population densities of both species, as measured by either estimate, fluctuated on the study areas from 1974 through 1977 (Tables 3 and 4, Fig. 5). Densities of male and female tree lizards and canyon lizards varied concomitantly from 1974 through 1977 (Fig. 5). The density estimates declined in the years characterized by low rainfall (1975 and 1977) and increased in the years characterized by higher rainfall (1974 and 1976). The variation in density was greater in *S. merriami* than in *U. ornatus* (Fig. 5).

AGE STRUCTURE.—The age structure data for posthatchling animals from the control publications of *S. merriami* and *U. ornatus* are presented in Fig. 6. In both species there was no difference in age structure between males and females in any year on either plot. The age vectors for the different plots did

TABLE 3

SUMMARY OF THE NUMBER AND DENSITY OF ADULT *U. ORNATUS* ON THE STUDY PLOTS (I AND IV) FOR EARLY JUNE OF 1974 - 1977. AC IS THE NUMBER OF ANIMALS ACTUALLY REGISTERED ON EACH AREA. LP IS THE SMALL SAMPLE LINCOLN-PETERSON ESTIMATE (CHAPMAN, 1951; SEBER, 1973) OF THE NUMBER OF RESIDENTS. DEN (AC) AND DEN (LP) ARE THE DENSITIES BASED ON ANIMALS ACTUALLY CAPTURED AND THE LINCOLN-PETERSON ESTIMATES RESPECTIVELY. DENSITY ESTIMATES BASED ON THE POOLED DATA FROM BOTH PLOTS ARE ALSO PRESENTED.

SEX	YEAR	PLOT #	AC	LP	DEN (AC)	DEN (LP)	DEN (AC)	DEN (LP)	
MALES	1974	I	20	32.00	37.88	60.61	31.03	45.07	
		IV	22	29.00	26.65	32.28			
	1975	I	16	22.80	30.30	43.18	28.66	36.05	
		IV	22	26.00	26.65	31.49			
	1976	I	20	21.20	37.88	40.15	36.20	44.08	
		IV	29	38.47	35.13	46.60			
	1977	I	8	8.00	15.15	15.15	22.16	20.87	
		IV	22	20.25	26.65	24.53			
	FEMALES	1974	I	19	22.00	35.98	41.67	24.38	34.48
			IV	14	24.67	16.96	29.88		
1975		I	10	16.00	18.94	30.30	22.16	26.60	
		IV	20	20.00	24.22	24.22			
1976		I	12	18.00	22.73	34.09	23.64	34.28	
		IV	20	28.40	24.22	34.40			
1977		I	6	6.00	11.36	11.36	17.73	20.64	
		IV	18	24.00	21.80	29.07			

not vary among years in either species. When the data for the two sexes were pooled for analysis, the fraction of yearling animals varied significantly among the four years of this study in both the canyon lizard ($\chi^2_1 = 55.04$; $p \leq 0.00001$) and the tree lizard ($\chi^2_1 = 27.96$; $p \leq 0.00001$). There are, of course, complementary changes in the proportion of older animals. The age structures for the two species vary concordantly, and the variation appears cyclical with proportion of yearlings being low in 1975 and 1977. Both of these are characterized by low precipitation and prey abundance, and both follow years of high egg production (see following section). It is probable that the number and, hence, proportion of animals in the yearling class was

TABLE 4
SUMMARY OF THE NUMBER AND DENSITY OF ADULT *S. MERRIAMI* ON THE STUDY PLOTS (I AND IV) FOR EARLY JUNE OF 1974 - 1977.
TERMINOLOGY IS AS IN TABLE 3.

SEX	YEAR	PLOT #	AC	LP	DEN (AC)	DEN (LP)	DEN (AC)	DEN (LP)
MALES	1974	I	36	40.50	68.18	76.70	68.71	63.41
		IV	57	45.33	69.04	54.91		
	1975	I	37	35.53	70.08	66.91	48.76	63.68
		IV	29	50.67	35.13	61.37		
	1976	I	47	43.75	89.02	82.86	78.31	80.90
		IV	59	65.75	71.46	79.64		
	1977	I	29	33.29	54.92	63.05	45.07	49.60
		IV	32	33.85	38.76	41.00		
	1974	I	34	41.50	64.39	78.60	47.28	57.62
		IV	30	36.50	36.34	44.21		
	1975	I	25	32.00	47.35	60.61	40.63	46.54
		IV	30	31.00	36.34	37.55		
1976	I	47	46.34	89.02	87.77	62.80	64.52	
	IV	38	41.00	46.03	49.66			
1977	I	29	37.00	54.92	70.08	45.80	46.33	
	IV	33	25.71	39.97	31.14			
FEMALES								

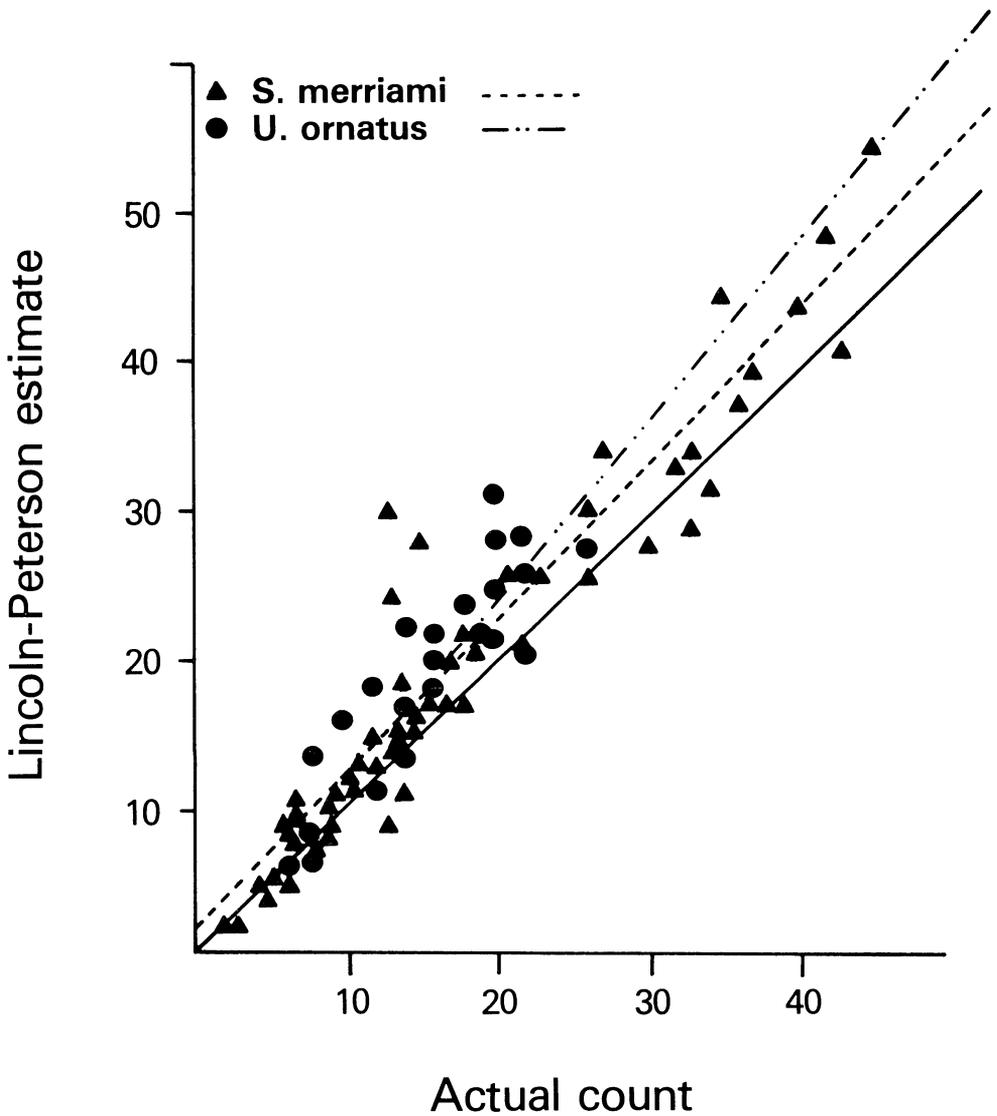


Fig. 4 Relationship between the small sample Lincoln-Peterson estimates of population size to the number of marked animals known to reside on a given study plot. The diagonal line represents the set of points for which the two estimates are equal. The regression model for *U. ornatus* is $Y = 0.5498 + 1.2262(X)$. The regression model for *S. merriami* is $Y = 1.5189 + 1.0549(X)$. The coefficient of determination of the model for *U. ornatus* is 0.79, and that of the model for *S. merriami* is 0.92.

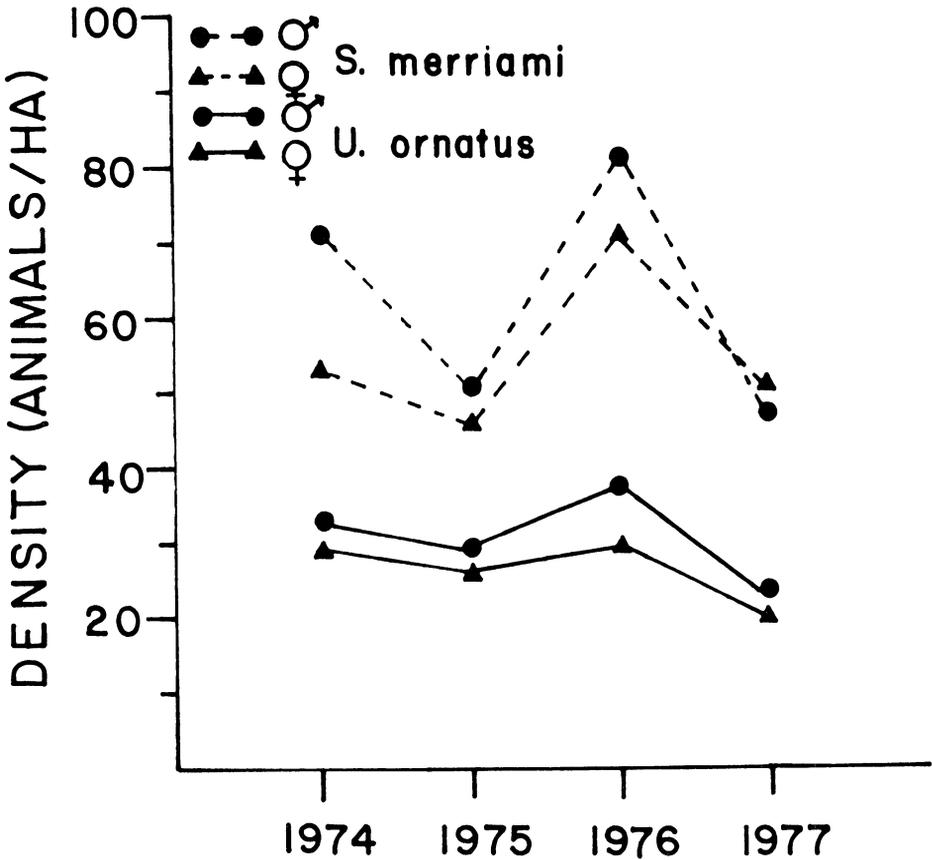


Fig. 5 Early June population densities of marked *S. merriami* and *U. ornatus* for 1974 - 1977. Data from both study plots were combined and these estimates were based on the number of animals actually censused on each area.

overestimated in 1974 due to the difficulty of accurately aging animals in the first year of the study. This problem was more extreme in *U. ornatus* because overlap in the size distributions of yearlings and older animals was greater in this species.

FECUNDITY

BASIC REPRODUCTIVE PATTERN AND CLUTCH FREQUENCY.—The following interpretation is based on the data obtained from the repeated recapture of individually marked females and from autopsies of animals sampled throughout the active seasons of the 4 years of this study. The data from 1976 (Fig. 7) are typical and are based on females for which the date of

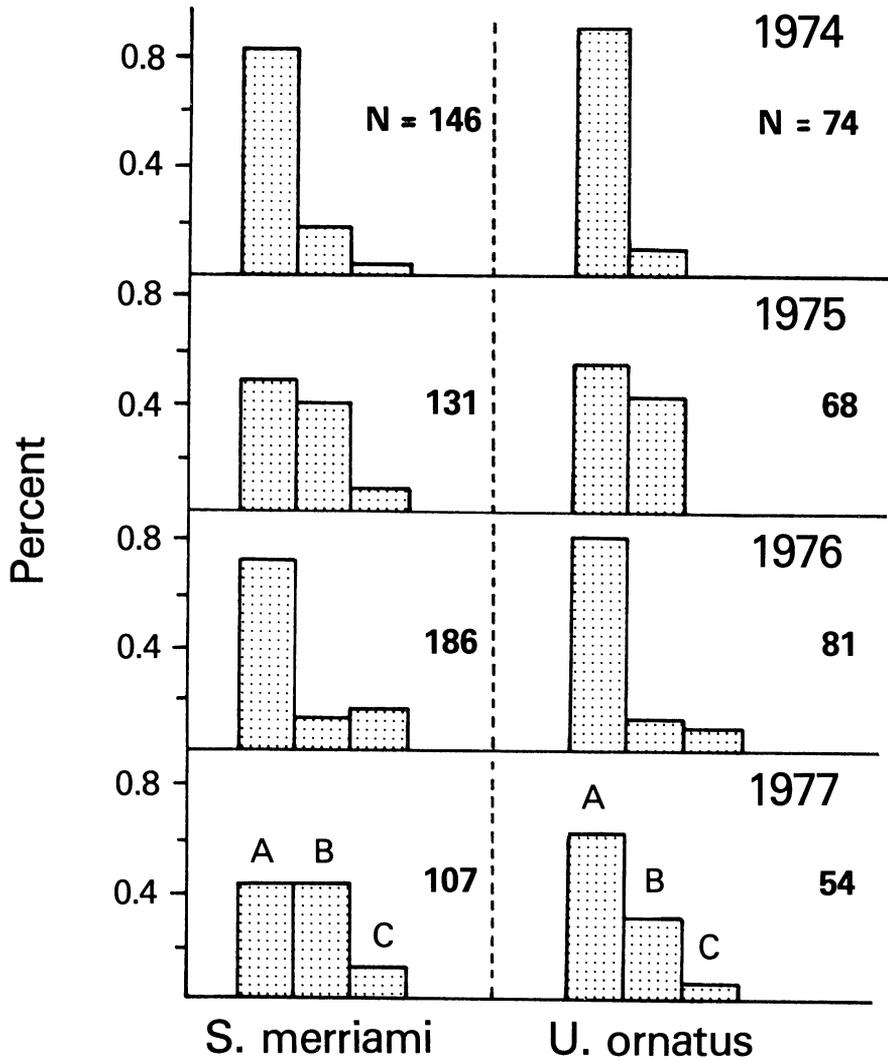


Fig. 6 Age structure of the study populations of *S. merriami* and *U. ornatus* for 1974 - 1977. Data on males and females are pooled. Animals denoted by A are yearlings, B denotes animals 2-3 years old, and C denotes animals ≥ 3 years old.

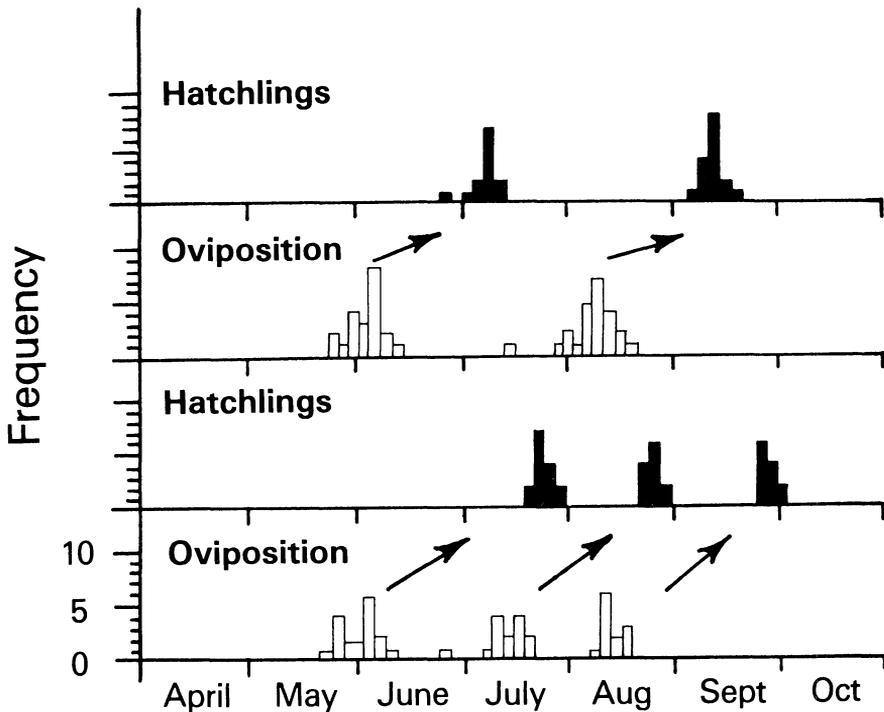


Fig. 7 Summary of data on model dates of oviposition and appearance of hatchlings in 1976. Data for *S. merriami* are in the top two panels, those for *U. ornatus* in the bottom two. Each bar represents a 3 day interval. See text for details.

oviposition was known to within 5 days. Following oviposition, females were frequently seen to have mud caked on their feet and chin. Occasionally females were captured twice within a few days and, based on palpation, had oviposited in the interval between captures. Females of these 2 types were used to estimate frequency distributions of the dates of oviposition throughout the active season. Frequency distributions of dates of hatching were estimated from the dates of capture of animals less than 30 mm SVL. Incubation period for a given clutch was estimated as the time between the modal date of oviposition and the modal date of hatching. The time required to develop the second or third clutch of the year was estimated as the time between the modal date of oviposition of that clutch and the modal date of oviposition of the preceding clutch. The time required to yolk the first clutch was estimated as the time from the 15th of April to the modal date of oviposition of the first clutch. These are probably overestimates because females may carry oviductal eggs for a varying period of time prior to oviposition of the first clutch. Autopsy of females of both species collected between 12-18 April, 1976 showed the initiation of yolk deposition and no evidence of a previous clutch that year (e.g., corpora lutea or enlarged, flaccid oviducts). Females collected after the third week in August in all years of the study were reproductively quiescent and showed no evidence of vitellogenesis for a later clutch.

Both species are oviparous and reproduce in the year following hatching at an age of about 11-13 months. Both initiate activity in the early spring and exhibit yolk deposition in ovarian follicles after the middle of April. Mating behavior was observed from mid-April through the beginning of August.

In the *S. merriami* populations studied here there are normally two clutches per active season. Oviposition of the first clutch typically occurs between 20 May and 15 June with hatchlings appearing about 30-40 days after oviposition. In 1976 the modal date of oviposition was estimated (Fig. 7) to be 7 June and the modal date of hatchling capture was estimated as 12 July, providing an estimate of incubation time of 35 days. Both sexes hatch at approximately 22 mm SVL. Oviposition of the second clutch normally occurs between 20 July and 20 August with hatchlings from this clutch appearing in late August to mid-September. In 1976 the modal date of oviposition of the second clutch was estimated as 11 August and the modal date of appearance of hatchlings was 14 September (Fig. 7), providing an estimate of 34 days incubation time.

In the *U. ornatus* populations from the Grapevine Hills three clutches are normally produced per year. The first clutch is typically laid in late May through early June, the second clutch in early- to mid-July, and the third clutch from mid- to late-August. In 1976, the modal date of oviposition was 5 June for the first clutch, 16 July for the second clutch, and 14 August for the third clutch (Fig. 7). In 1976, the modal date of hatchling capture was 14 July for the first clutch, 26 August for the second clutch and 27 September for the third clutch. These data provided estimates of incubation times of 50 days for the first, 41 days for the second, and 44 days for the final clutch. Vitellogenesis for the first clutch was estimated to require 51 days, 41 days for the second clutch, and 29 days for the final clutch (Fig. 7).

Based on the presence of yolked follicles or oviductal eggs, the smallest sexually mature female *U. ornatus* in the reproductive samples was 41 mm SVL; the smallest female *S. merriami* was 43 mm. All female *S. merriami* above 45 mm SVL during the breeding season were sexually mature and 8 of 18 (44.4%) that were 44 mm SVL and captured at the appropriate time of the year were sexually mature. All 8 of these 44 mm SVL mature animals were from 1974 or 1976 (wet years), and in those years 8 of 11 (73%) females of this size showed evidence of sexual maturity.

AGE-SPECIFIC FECUNDITY.—Predicted clutch sizes of females of a given body size (SVL) were calculated from the regression models of clutch size on SVL obtained from destructive samples of females taken throughout the study. Separate regression models were calculated for the first and later clutches of each year and compared using the one-way analysis of covariance (ANCOVA). The regression models for 1975 and 1977 did not differ significantly for either species and data were pooled and used to estimate a single model for each clutch for each species. The same was true of the models for 1974 and 1976. The form of the clutch size regression models is different for the two species. It was necessary to estimate the clutch size regression models for *U. ornatus* from logarithmically transformed data to

TABLE 5

REGRESSION MODELS USED TO PREDICT THE CLUTCH SIZE OF *U. ORNATUS* AND *S. MERRIAMII* FROM SVL. ALL MODELS ARE OF THE FORM $\ln Y = a(\ln X) + b$, WHERE Y IS THE EXPECTED CLUTCH SIZE OF A FEMALE OF SVL = X. R² IS THE COEFFICIENT DETERMINATION. *** implies $p \leq 0.001$; ** implies $p \leq 0.01$.

Species	Model	a	b	R ²	F
<i>S. merriami</i>	Clutch I	1.889	-5.916	0.72	F _{1,48} = 96.01***
	Clutch II	1.367	-3.844	0.76	F _{1,49} = 104.32***
	Wet years	1.336	-3.721	0.57	F _{1,48} = 62.62***
	Dry years	2.210	-7.254	0.80	F _{1,49} = 191.79***
<i>U. ornatus</i>	Clutch I	2.622	-8.591	0.63	F _{1,34} = 14.26***
	Clutch II, III	2.571	-8.420	0.74	F _{1,55} = 63.11***
	Wet years	2.407	-7.693	0.56	F _{1,59} = 7.36**
	Dry years	2.910	-9.873	0.77	F _{1,30} = 101.64***

obtain a homoscedastic distribution of the residuals. These models and the relevant statistics are summarized in Table 5. The clutch size regression models for *S. merriami* were derived by computing the mean clutch size for each mm of body size (SVL) and then calculating a weighted regression of the logarithmically transformed variables mean clutch size and SVL. Each pair of observations (mean clutch size, SVL) was weighted by the number of females of that body size in the data set. This treatment produced models with a satisfactory distribution of residuals and the largest coefficient of determination (R²). These models are summarized in Table 5. A simple linear regression using the raw fecundity data for *S. merriami* or using logarithmically transformed raw data resulted in models which systematically overestimated the clutch size of small animals and correspondingly underestimated the clutch size of large animals. The models utilized here provide the most accurate predictions of clutch size for a given body size (SVL) among the several types of linear models constructed.

In both species there is a significant relationship between body size as measured by SVL and the number of eggs a particular female is expected to produce (Fig. 8). The model for *U. ornatus* in 1974, 1976 (F_{1,59} = 7.36; $p \leq 0.0001$) explained 56% of the variance in clutch size among females; the model for 1975, 1977 (F_{1,30} = 101.64; $p \leq 0.0001$) explained 77% of the variance in clutch size among females (Table 5). The model for *S. merriami* in 1974, 1976 (F_{1,48} = 62.62; $p \leq 0.0001$) explained 80% of the variance in clutch size among females; the model for 1975, 1977 (F_{1,49} = 191.79; $p \leq 0.0001$) explained 80% of the variance (Table 5).

The analysis of covariance (ANCOVA) revealed that the clutch size for a given SVL varied significantly among years in both species. The model for

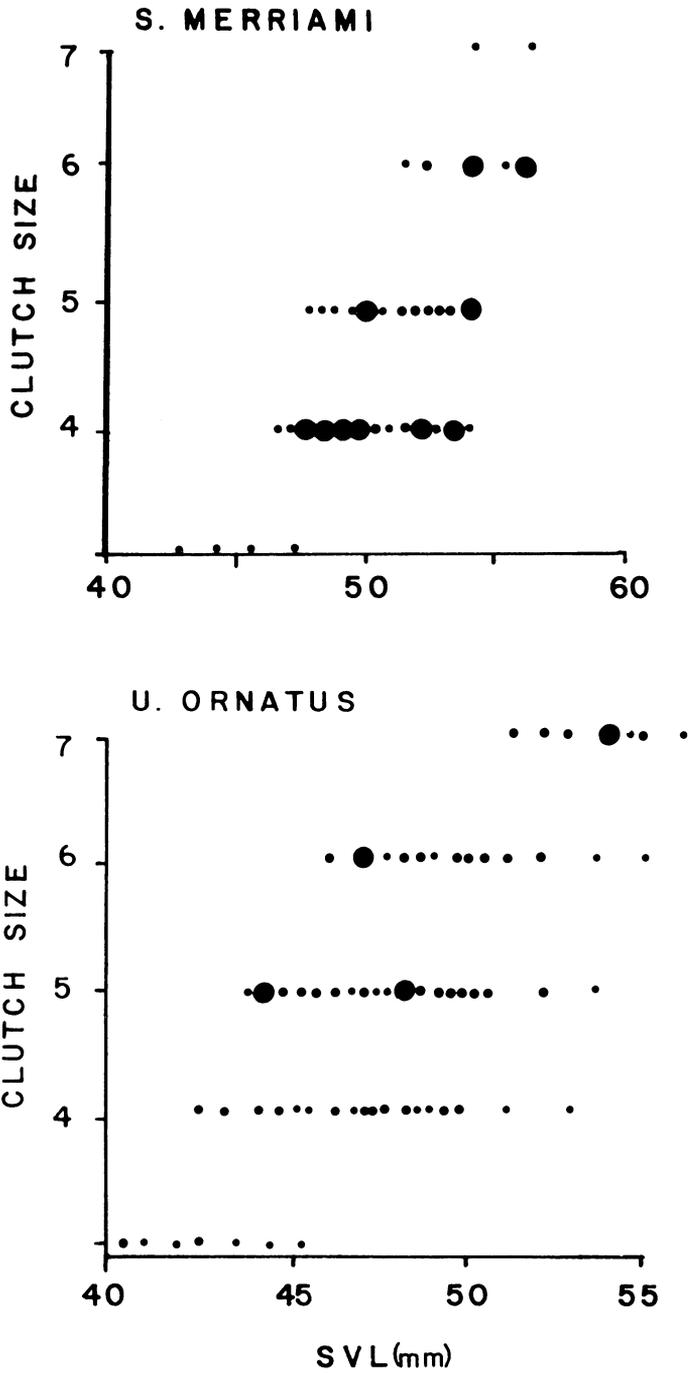


Fig. 8 Relationship of clutch size to body size (SVL) in *S. merriami* and *U. ornatus*. Data from all years are shown. Smallest dots indicate 1 data point, medium indicate 2-5 data points, and largest indicate > 5 data points.

U. ornatus in the wet years (1974, 1976) was significantly different from that characterizing dry (1975, 1977) years ($F_{2,89} = 28.38$; $p \leq 0.0001$). The models do not differ in slope ($F_{1,89} = 1.29$; $p \leq 0.26$), and hence the difference is one of intercept. The expected clutch size of a 50 mm SVL female in the wet years was 5.6 while that of the same female in the dry years was 4.5. The model for *S. merriami* in the wet years was significantly different from that characterizing the dry years ($F_{2,99} = 21.46$; $p \leq 0.0001$). Again the models do not differ in slope ($F_{1,99} = 1.26$; $p \leq 0.73$), and hence the difference is one of intercept. The expected clutch size of a 50 mm SVL female canyon lizard in the wet years was 4.5 while that of the same female in the dry years was 4.1.

In *S. merriami* the expected clutch size for females of a given SVL depends on which clutch of the year is being produced. There is a highly significant relationship between clutch size and SVL in both the first ($F_{1,50} = 27.05$; $p \leq 0.0001$) and second ($F_{1,49} = 48.20$; $p \leq 0.0001$) clutches in any year. The regression model for the first clutch accounts for 72% of the variance in clutch size, and the model for clutch two accounts for 76% of the variance in clutch size. The regression models are significantly different for the two clutches ($F_{2,97} = 5.4$; $p \leq 0.005$) and in this case the slopes of the models differ significantly ($F_{1,97} = 6.45$; $p = 0.013$). The expected clutch size for a 50 mm (SVL) female producing the second clutch of the year is 4.5 eggs. This effect is minor compared to the differences between wet and dry years. My data do not reveal a significant difference in clutch size for a given SVL (ANCOVA) between first and later clutches for *Urosaurus ornatus*.

The regression models of Table 5 were used to estimate the total egg production on each of the study plots for each year of the study from the estimated number of females inhabiting each area and the distribution of body sizes of females on each plot at the time each clutch was produced. In these estimations, 41 mm was taken as the minimum sexually mature body size in *U. ornatus* and all female *S. merriami* 44 mm SVL or larger were assumed to be sexually mature. Three clutches per year were assumed for *U. ornatus*, two clutches in *S. merriami*. These estimates are presented in Tables 6 and 7.

The mean body size (SVL) of sexually mature females inhabiting the study plots (I and IV) varied among years and seasonally in both species. Body size did not vary between study plots and data from wet (1974, 1976) years were pooled for analysis, as were data from dry years (1975, 1977). Data from May and June were used to estimate the body size for sexually mature *S. merriami* and *U. ornatus* producing the first clutch and data from July and August were used to estimate the body size of females of each species producing the second and later clutches of each year.

In both species, the mean body size (SVL) of females producing the first clutch of the year was greater than that of females producing the later clutches ($F_{1,171} = 14.08$; $p \leq 0.0001$ for *U. ornatus* and $F_{1,246} = 14.88$; $p \leq 0.0001$ for *S. merriami*) in all years. Body size of reproductive females was greater in wet years (1974, 1976) in *S. merriami* for both clutch I ($F_{1,301} =$

TABLE 6

SUMMARY OF ESTIMATED ANNUAL (1974 - 1976) EGG PRODUCTION BY *S. MERRIAM* RESIDING ON EACH STUDY PLOT. SVL IS THE ESTIMATED MEAN SVL OF FEMALES PRODUCING EACH CLUTCH. THE NUMBERS IN PARENTHESES ARE 95% CONFIDENCE INTERVAL HALF WIDTHS. ESTIMATES ARE BASED ON THE APPROPRIATE REGRESSION MODEL (TABLE 5) RELATING MEAN CLUTCH SIZE TO SVL.

YEAR	STUDY AREA	CLUTCH I		CLUTCH II		TOTAL	
		EGGS	SVL	EGGS	SVL	EGGS	SVL
1974	I	123.15	49.25 (1.04)	127.68	50.50 (0.85)	250.83	49.86 (1.26)
	IV	80.59	47.90 (0.93)	107.04	49.68 (0.94)	187.63	48.88 (1.80)
1975	I	78.86	50.91 (1.04)	79.07	51.24 (1.34)	157.93	51.07 (0.33)
	IV	110.24	50.24 (1.07)	90.93	51.20 (1.31)	203.17	50.67 (0.96)
1976	I	118.06	50.02 (1.31)	152.77	51.77 (1.00)	270.84	50.59 (0.52)
	IV	99.02	49.61 (1.32)	156.09	50.75 (0.89)	255.12	50.29 (1.14)

TABLE 7

SUMMARY OF ESTIMATED ANNUAL EGG PRODUCTION (1974-1976) BY *U. ORNATUS* RESIDING OF EACH STUDY PLOT. SVL IS THE ESTIMATED MEAN SVL OF THE FEMALES PRODUCING EACH CLUTCH. NUMBERS IN PARENTHESES ARE 95% CONFIDENCE INTERVAL HALF WIDTHS. ESTIMATES ARE BASED ON THE APPROPRIATE REGRESSION MODEL (TABLE 5) RELATING CLUTCH SIZE TO SVL.

YEAR	STUDY AREA	CLUTCH I		CLUTCH II		CLUTCH III		TOTAL	
		EGGS	SVL	EGGS	SVL	EGGS	SVL	EGGS	SVL
1974	I	97.84	47.25 (0.74)	73.15	48.55 (0.86)	61.46	49.90 (1.06)	232.45	48.30 (2.16)
	IV	73.09	43.72 (0.82)	73.31	46.00 (0.52)	80.30	47.77 (0.48)	226.67	45.75 (3.39)
1975	I	37.22	46.60 (1.86)	28.27	48.00 (1.35)	25.40	48.80 (1.23)	90.90	47.60 (1.90)
	IV	81.23	48.10 (0.86)	52.02	49.20 (0.91)	36.92	50.30 (0.58)	170.17	48.87 (1.74)
1976	I	49.65	47.50 (1.60)	59.94	47.58 (1.77)	53.70	49.08 (1.40)	163.29	47.54 (0.80)
	IV	92.84	46.15 (1.30)	85.23	47.70 (1.03)	75.56	49.20 (0.94)	253.62	47.50 (2.49)

15.91; $p \leq 0.0001$) and clutch II ($F_{1,264} = 12.31$; $p \leq 0.0005$). In *U. ornatus*, the body size of reproductive females was greater in wet years than in dry ones for the first clutch ($F_{1,92} = 6.98$; $p = 0.0097$); however, there was no significant difference among years in mean SVL at the time later clutches were produced.

Mean egg volume did not differ significantly between wet (1974, 1976) and dry (1975, 1977) years ($F_{1,88} = 0.43$; $p > 0.5$ for *S. merriami* and $F_{1,71} = 1.69$; $p > 0.2$ for *U. ornatus*) in either species. Mean egg volume for *S. merriami* in wet years (1974, 1976) was 229.61 ± 7.66 (95% CI) mm^3 , that for the dry years (1975, 1977) was 217.51 ± 10.57 mm^3 . Mean egg volume for *U. ornatus* in wet years was 156.64 ± 6.27 mm^3 , that for dry years was 149.35 ± 9.19 mm^3 . The two species differed ($F_{1,158} = 171.68$; $p \leq 0.0001$) in egg volume when data from all years were pooled. The mean egg volume for *S. merriami* was 220.00 ± 6.19 mm^3 , that for *U. ornatus* was 156.80 ± 6.22 mm^3 .

There was no significant correlation between individual egg wet weight (EWW), individual egg dry weight (EDW), or percent water content of individual eggs (PWC) and the number of eggs in a given clutch in either the wet (1976) or dry (1977) years in either species. Likewise, there were no significant differences between wet and dry years in EWW, EDW, or PWC for either species (F tests; all $p > 0.05$). Mean EWW, EDW, and PWC data for both species are summarized in Table 8. Data for 1976 and 1977 were combined and the two species contrasted. EWW and EDW were highly correlated in both species ($r = 0.91$, $p \leq 0.001$ for *S. merriami*; $r = 0.76$, $p \leq 0.001$ for *U. ornatus*). *S. merriami* had significantly larger EWW ($F_{1,129} = 250.0$; $p \leq 0.0001$) and EDW ($F_{1,129} = 584.4$; $p \leq 0.0001$) than *U. ornatus*. PWC, on the other hand, was significantly lower ($F_{1,129} = 527.9$; $p \leq 0.0001$) in *S. merriami*.

MALE REPRODUCTIVE PATTERNS.—The smallest male *U. ornatus* showing evidence of sexual maturity (enlarged testes with visible seminiferous tubules) was 40 mm SVL and the smallest sexually mature male *S. merriami* was 43 mm SVL. All male *U. ornatus* larger than 43 mm SVL and all *S. merriami* larger than 45 mm SVL were sexually mature, indicating that males of both species attain sexual maturity at about the same size and age as females.

Data on the seasonal cycle of testes size are summarized for adults of both species in Fig. 9. The greatest length of the left testis expressed as a percent of SVL was used as an index of testis size. Pairwise Mann-Whitney U tests were used to compare data from wet and dry years. Median testis size did not differ between wet and dry years in either species for any month of the study. Pairwise comparison of the combined data revealed that in every month for which there were data, testes of adult *U. ornatus* comprised a greater percentage of SVL than was the case for *S. merriami* (Mann-Whitney U tests; all $p \leq 0.001$).

The seasonal cycles of testis size of both species are strikingly similar (Fig. 9). Sexually mature males of both species apparently emerge from hibernation with testes at or near maximum size. Courtship behavior was observed

TABLE 8
 SUMMARY OF DATA ON MEAN INDIVIDUAL EGG WET WEIGHT (EWW), EGG DRY WEIGHT (EDW), AND PERCENT WATER
 (PCW) FOR *SCELOPORUS MERRIAMII* AND *UROSAURUS ORNATUS*. DATA FOR WET (1976) AND DRY (1977) YEARS ARE PRESENTED.
 NUMBERS IN PARENTHESES ARE SAMPLE SIZES.

	WET YEAR (1976)	DRY YEAR (1977)	COMBINED
<i>S. merriami</i>			
EWW	0.2074 ± 0.0111 (52)	0.1997 ± 0.0128 (47)	0.2039 ± 0.0064 (104)
EDW	0.0994 ± 0.0051 (57)	0.0958 ± 0.0046 (47)	0.0978 ± 0.0027 (104)
PCW	52.05 ± 0.03 (57)	52.00 ± 0.04 (47)	52.03 ± 0.20 (104)
<i>U. ornatus</i>			
EWW	0.1459 ± 0.0201 (38)	0.1562 ± 0.0184 (24)	0.1510 ± 0.0074 (62)
EDW	0.0560 ± 0.0082 (38)	0.0654 ± 0.0093 (24)	0.0607 ± 0.0051 (62)
PCW	61.38 ± 0.04 (38)	58.09 ± 0.04 (24)	59.73 ± 0.02 (62)

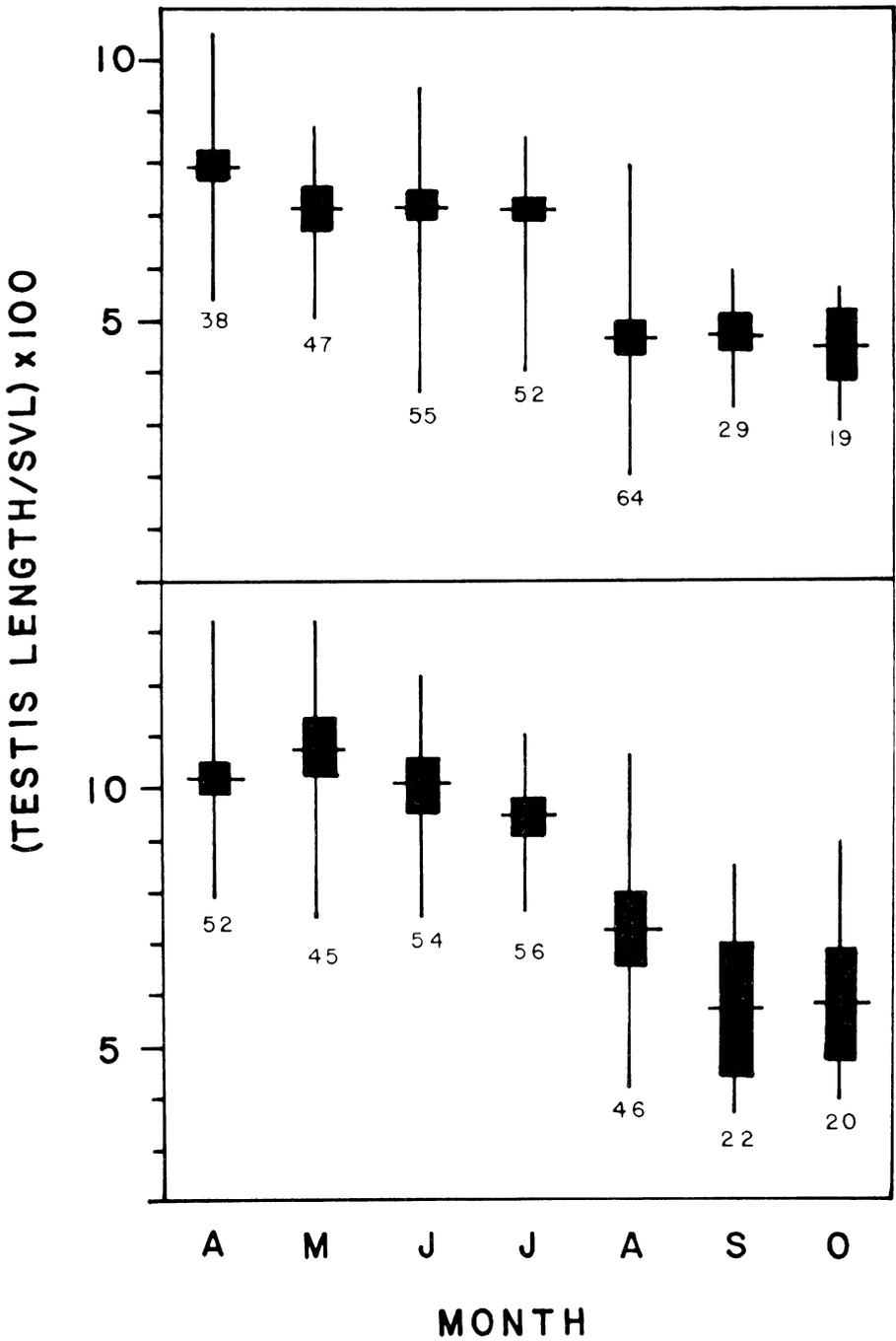


Fig. 9 Seasonal cycle of testis size for *S. merriami* (top) and *U. ornatus*. Data from 1976 and 1977 shown. Vertical line indicates the range, horizontal line is the mean, and vertical bar is the 95% confidence interval. Numbers indicate sample size.

in both species from early–mid April through early August and testes were enlarged throughout this period. Gonadal regression begins in early August in *S. merriami* and in mid – late August in *U. ornatus*. Cessation of courtship behavior was observed to occur synchronously with testicular regression in both species. Testes of adult males of both species were completely regressed in September and October.

SUMMARY OF REPRODUCTION.—The canyon lizard and tree lizard populations inhabiting the Grapevine Hills exhibit strikingly similar annual reproductive cycles. Both species are active in early April. Courtship behavior is observed in both species from April through the beginning of August. The first clutch is oviposited in late May or early June and usually coincides with periods of increased precipitation; the canyon lizard typically produces a second clutch in late July to mid-August. Hatchlings normally emerge about 35 days after oviposition and average about 22 mm SVL. The tree lizard normally produces three clutches per year; in late May or early June, in mid-July, and in mid-August to early September. The incubation period for tree lizard eggs was estimated to be between 41 and 50 days, slightly longer than in the canyon lizard (about 35 days). Tree lizards of both sexes averaged about 20 mm SVL at hatching. The clutch size for a given body size is greater in the tree lizard; for example, a female *U. ornatus* which is 50 mm SVL is expected to produce a first clutch of 5.6 eggs in a wet year. A female canyon lizard of the same SVL is expected to produce a clutch of 4.4 eggs under the same conditions. Individual egg volumes differ in the two species with the mean egg volume of the canyon lizard ($220.0 \pm 6.2 \text{ mm}^3$ [95% CI]) being significantly ($F_{1,138} = 171.68$; $p \leq 0.0001$) larger than that of the tree lizard ($156.6 \pm 6.2 \text{ mm}^3$). Thus, for the first clutch of a wet year, the expected volume of the clutch of a female tree lizard which has a SVL of 50 mm would be 877.1 mm^3 while that of a canyon lizard of the same body size would be 961.4 mm^3 . Expected clutch size increases more quickly with body size in *S. merriami* than in *U. ornatus*.

The reproductive response of these two species to yearly variation in precipitation was concordant. In the dry years (1975, 1977), sexually mature females were smaller in average body size, produced fewer eggs for a given body size, and produced fewer total eggs than in the wet years (1974, 1976).

SURVIVORSHIP

Annual survivorship of adult lizards was measured from the beginning of June of one year to the beginning of June of the following year. This time was chosen because it is approximately the average date of oviposition of the first clutch in both the tree lizard and the canyon lizard. Minimal annual survival of each post-hatchling age class was estimated from data on the number of animals known to be alive on a particular study area in June of one year and which were recaptured the following year. First year survivorship was measured from estimates of the number of eggs produced on a

particular study area in one year and the number of yearlings captured on that area in the following year. I attempted to partition first year survival and hatchling survival. This was done for *S. merriami* by computing small sample Lincoln-Peterson estimates of the number of hatchlings produced and estimating egg survival from those estimates and the estimates of the number of eggs which gave rise to that cohort of hatchlings. Frequently, due to small numbers of hatchlings captured, estimates from particular clutches or study areas could not be computed. This problem was particularly acute in *U. ornatus*, and this method could not be used for this species either due to low numbers of marked hatchlings or because yearling cohorts (yearlings from different clutches the previous year) could not be identified, making the size of the egg pool impossible to determine. Hatchling survival was estimated for both species as the proportion of marked hatchlings that were recaptured as yearlings on a particular area.

ANNUAL ADULT SURVIVORSHIP.—The minimal annual survivorship estimates for all post-hatchling age classes (animals which are yearlings or older) are presented in Tables 9 and 10 for male and female *S. merriami*; in

TABLE 9
MINIMUM ANNUAL SURVIVORSHIP ESTIMATES, P(S), FOR MALE *SCELOPORUS MERRIAMII*. AGE CLASSES ARE TABULATED SEPARATELY. M IS THE NUMBER OF ANIMALS INITIALLY MARKED; S IS THE NUMBER RECAPTURED AFTER ONE YEAR. FOR THE 0 - 1 AGE CLASS, M IS THE ESTIMATED EGG PRODUCTION (TABLE 6). ESTIMATES ARE BASED ON DATA FROM BOTH STUDY AREAS. SEE TEXT FOR DETAILS.

YEAR	AGE	0 - 1	1 - 2	2 - 3	3 - 4	4 - 5
1974	M	404.88	141	29	5	—
	S	52	85	17	2	—
	P(S)	0.128	0.603	0.586	0.400	—
1975	M	325.96	52	85	17	2
	S	149	27	42	9	0
	P(S)	0.451	0.519	0.494	0.529	0.000
1976	M	559.72	149	27	42	9
	S	58	54	7	12	0
	P(S)	0.104	0.362	0.259	0.286	0.000
TOTAL	M	1290.56	342	141	64	11
	S	259	166	66	23	0
	P(S)	0.201	0.485	0.468	0.359	0.000

TABLE 10

MINIMUM ANNUAL SURVIVORSHIP ESTIMATES, P(S), FOR FEMALE *S. MERRIMAI*. AGE CLASSES ARE TABULATED SEPARATELY. LABELING CONVENTIONS ARE AS IN TABLE 9. FOR THE 0 - 1 AGE CLASS, M IS THE ESTIMATED EGG PRODUCTION (TABLE 6). ESTIMATES ARE BASED ON DATA FROM BOTH STUDY AREAS. SEE TEXT FOR DETAILS.

YEAR	AGE	0 - 1	1 - 2	2 - 3	3 - 4	4 - 5
1974	M	404.88	113	14	1	-
	S	54	36	6	0	-
	P(S)	0.133	0.319	0.429	0	-
1975	M	325.96	54	36	6	-
	S	138	19	14	4	-
	P(S)	0.423	0.352	0.389	0.667	
1976	M	559.22	138	19	14	4
	S	45	35	3	3	2
	P(S)	0.080	0.254	0.158	0.286	0.500
TOTAL	M	1290.56	305	69	21	
	S	237	90	23	7	
	P(S)	0.184	0.295	0.333	0.333	

Tables 11 and 12 for male and female *U. ornatus*. These estimates are probably close to the true survivorship due to the high sampling effort and high average catchability of the lizards. Recapture analysis (Table 1) indicated that female *U. ornatus* were the least catchable of the post-hatchling lizards studied. Approximately 18% of the resident tree lizard females on any particular area escaped capture in any given year. My estimates of minimum annual survival should correspondingly underestimate the true annual survivorship by the greatest amount in these animals.

Minimal annual survivorship did not vary significantly (χ^2 tests; all $p < 0.1$) among age classes in post-hatchling male or female *S. merriami* or in female *U. ornatus* in any year of the study. Post-hatchling survivorship of male *U. ornatus* did not differ significantly among year classes in 1974 ($\chi^2_1 = 0.39$; $p > 0.5$) or 1975 ($\chi^2_1 = 0.007$; $p > 0.5$). However, yearling males suffered significantly higher mortality than did older males ($\chi^2_1 = 12.16$; $p \leq 0.005$) in 1976.

TABLE 11
 MINIMUM ANNUAL SURVIVORSHIP ESTIMATES, P(S), FOR MALE
UROSAURUS ORNATUS. AGE CLASSES ARE TABULATED SEPARATELY.
 LABELING CONVENTIONS ARE AS IN TABLE 9. FOR THE 0 - 1 AGE
 CLASS, M IS THE ESTIMATED EGG PRODUCTION (TABLE 6).
 ESTIMATES ARE BASED ON DATA FROM BOTH STUDY AREAS.
 SEE TEXT FOR DETAILS.

YEAR	AGE	0 - 1	1 - 2	2 - 3	ALL ADULTS
1974	M	217.275	39	4	43
	S	22	16	1	17
	P(S)	0.101	0.410	0.250	0.395
1975	M	130.535	22	16	38
	S	38	6	5	11
	P(S)	0.291	0.273	0.313	0.290
1976	M	208.454	38	6	44
	S	22	10	6	16
	P(S)	0.106	0.263	1.000	0.364
TOTAL	M	556.264	99	26	124
	S	82	32	12	43
	P(S)	0.147	0.323	0.462	0.347

Annual post-hatchling survivorship in *U. ornatus* did not differ significantly among years in either males ($\chi^2_2 = 1.03$; $p > 0.1$) or female ($\chi^2_2 = 1.97$; $p > 0.1$). Male and female tree lizards did not differ significantly in minimal annual adult survivorship in any year of the study ($\chi^2_2 = 3.07$; $p > 0.6$).

There were statistically significant differences in annual post-hatchling survivorship of male ($\chi^2_2 = 31.23$; $p \leq 0.0001$) and female ($\chi^2_2 = 6.14$; $p \leq 0.05$) canyon lizards. Annual adult survival was significantly lower in male *S. merriami* in 1976 than in 1974 ($\chi^2_1 = 29.82$; $p \leq 0.0001$) and 1975 ($\chi^2_1 = 12.32$; $p \leq 0.0001$) though survival rates did not differ significantly in 1974 and 1975 ($\chi^2_1 = 2.96$; $p = 0.0852$). Annual adult survival was significantly lower in female *S. merriami* in 1976 than in 1975 ($\chi^2_1 = 5.82$; $p \leq 0.0159$); survival rates in 1974 did not differ significantly from those of

TABLE 12
 MINIMUM ANNUAL SURVIVORSHIP ESTIMATES, P(S), FOR FEMALE
U. ORNATUS. AGE CLASSES ARE TABULATED SEPARATELY.
 LABELING CONVENTIONS ARE AS IN TABLE 9. FOR THE 0 - 1 AGE
 CLASS, M IS THE ESTIMATED EGG PRODUCTION (TABLE 6).
 ESTIMATES ARE BASED ON DATA FROM BOTH STUDY AREAS.
 SEE TEXT FOR DETAILS.

YEAR	AGE	0 - 1	1 - 2	2 - 3	ALL ADULTS
1974	M	217.275	30	3	33
	S	16	14	0	14
	P(S)	0.074	0.467	0.000	0.424
1975	M	130.535	16	14	30
	S	26	4	5	9
	P(S)	0.199	0.250	0.357	0.300
1976	M	208.454	26	4	30
	S	16	6	2	8
	P(S)	0.077	0.231	0.500	0.267
TOTAL	M	556.264	72	21	93
	S	58	24	7	31
	P(S)	0.104	0.333	0.333	0.333

1975 ($\chi^2_1 = 0.79$; $p > 0.1$) or 1976 ($\chi^2_1 = 2.49$; $p \leq 0.1$). Adult male canyon lizards survived significantly better than adult females when data from all years are compared ($\chi^2_1 = 22.28$; $p < 0.0001$).

A number of authors including Pianka (1970), Parker and Pianka (1975), and Tinkle and Ballinger (1972) have used the frequency of broken or regenerated tails as an index of the intensity of predation experienced by different lizard populations. Tinkle and Ballinger (1972) correctly pointed out that comparison of raw data on tail break frequencies ignores differences in life expectancy and length of activity seasons which determine, in part, the amount of time an individual is exposed to predation and, hence, the risk of tail loss. Since the active seasons of these two species in the Grapevine Hills were not different and the cohort generation times were essentially the same (Tables 26 and 27), it was unnecessary to adjust the data

TABLE 13
OBSERVED TAIL BREAK FREQUENCIES, P(B), OF ADULT *S. MERRIAMI*
AND *U. ORNATUS*. DATA FROM BOTH STUDY PLOTS ARE COMBINED.
NUMBERS IN PARENTHESES ARE SAMPLE SIZES.

Species	Number broken	P(B)
<i>S. merriami</i>		
Males	195 (555)	.351
Females	104 (429)	.242
<i>U. ornatus</i>		
Males	107 (355)	.301
Females	75 (245)	.306

on tail break frequencies for comparison. The observed tail break frequency (Table 3) of adult male canyon lizards (0.351) was significantly higher ($\chi^2 = 13.57$; $p \leq 0.003$), than that of females (0.242). There was no significant difference in the proportion of broken tails between male (0.301) and female (0.306) tree lizards during this study (Table 13). Observed tail break frequencies as indicators of relative mortality rates among the sexes of *S. merriami* do not agree with the mortality rates estimated from demographic data. Adult male canyon lizards had significantly lower mortality rates (Table 10) than did adult females but higher tail break frequencies. Predator escape tactics employed by the two sexes may differ such that the probability of tail loss in an encounter with a predator is higher for males. The suite of predators attacking males could also differ from that attacking females. At any rate, these results indicate that the use of tail break frequencies to estimate relative mortality rates may lead to erroneous conclusions. Tail break frequencies of male and female tree lizards did not differ significantly, and the estimated mortality rates for the two sexes were not significantly different. There were no significant differences between canyon lizards and tree lizards in tail break frequencies or estimated mortality rates.

FIRST YEAR SURVIVORSHIP.—Survival rates of individuals of both species in their first year of life were estimated indirectly because I was unable to mark eggs. I employed two estimates of survival to June of the year following hatching. The first is based on the estimated number of eggs oviposited on a particular study area in a given year and the number of yearling animals captured on that area the following year. This method, therefore, provides a minimal estimate of first year survival. The second method employs the same estimate of egg production and the small sample Lincoln–Peterson estimate (Seber, 1973; Chapman, 1951) of the number of yearlings residing on the study area in early June of the following year. The estimates of first year survival based on these data are presented in Table 14 for both species. There were no significant differences in first year survival between males

TABLE 14

FIRST YEAR SURVIVAL OF *S. MERRIAMI* AND *U. ORNATUS*. ESTIMATES ARE BASED ON CAPTURES FROM BOTH STUDY AREAS. EGG PRODUCTION IS BASED ON THE REGRESSION MODELS RELATING FECUNDITY TO SVL (TABLE 5). TWO ESTIMATES OF THE NUMBER OF YEARLINGS ARE SHOWN. AC REPRESENTS THE ACTUAL NUMBER OF ANIMALS KNOWN TO HAVE SURVIVED TO AGE ONE. SURVIVORSHIPS BASED ON THIS ESTIMATE ARE MINIMAL VALUES. LP INDICATES THE SMALL-SAMPLE LINCOLN-PETERSON ESTIMATE OF THE NUMBER OF YEARLINGS.

SPECIES	YEAR	EGGS	NUMBER OF YEARLINGS		FIRST-YEAR SURVIVAL	
			AC	LP	AC	LP
<i>S. merriami</i>	1974	809.76	106	119.75	0.13	0.15
	1975	651.91	287	291.01	0.44	0.45
	1976	1118.44	103	114.24	0.09	0.13
	TOTAL	2581.11	496	555.00	0.19	0.22
<i>U. ornatus</i>	1974	434.55	38	80.00	0.09	0.18
	1975	261.07	64	69.23	0.25	0.27
	1976	416.91	38	48.25	0.09	0.12
	TOTAL	1112.53	140	197.48	0.13	0.18

and females of either species during any year of the study, and the data from both sexes are pooled in Table 15 and for further analysis. The estimates of first year survival based on these two methods are highly correlated ($r = 0.98$; $p \leq 0.01$).

Both *S. merriami* ($\chi^2_2 = 349.92$; $p \leq 0.0001$) and *U. ornatus* ($\chi^2_2 = 44.25$; $p \leq 0.0001$) experienced significantly different first year mortality among the years of this study. In *S. merriami* all pairwise comparisons of first year survival between years revealed highly significant statistical differences (χ^2 tests; all $p \leq 0.007$), and the minimal first year survival in 1975 (0.44) was dramatically higher than in either 1974 (0.13) or 1976 (0.09). The same basic pattern was apparent in the data for *U. ornatus*. The minimal survival rates for first year tree lizards were higher in 1975 than in 1974 ($\chi^2_1 = 32.50$; $p \leq 0.0001$) or 1976 ($\chi^2_1 = 29.82$; $p \leq 0.0001$); estimates of first year survival for 1974 did not differ significantly from those of 1976 ($\chi^2_1 p > 0.8$).

First year survival differed significantly between these two species ($\chi^2_2 = 24.05$; $p \leq 0.0001$) when data from all years were compared, with *S. merriami* experiencing lower first year mortality, especially in 1975. Pairwise comparisons of first year survival revealed significant differences in 1974

TABLE 15

SUMMARY OF EGG SURVIVAL ESTIMATION FOR *S. MERRIAMII* BASED ON THE SMALL SAMPLE LINCOLN-PETERSON (CHAPMAN, 1951; SEBER, 1973) ESTIMATES OF THE NUMBER OF HATCHLINGS THAT EMERGED ON THE STUDY AREAS. DUE TO LOW SAMPLE SIZES OF MARKED HATCHLINGS, NOT ALL CLUTCHES COULD BE ANALYZED. N_1 IS THE NUMBER OF HATCHLINGS MARKED IN THE ORIGINAL SAMPLE, N_2 IS THE NUMBER OF YEARLINGS FROM THE ORIGINAL CLUTCH THAT WERE CAPTURED THE FOLLOWING SPRING, AND M_2 IS THE NUMBER OF MARKED ANIMALS IN THE SECOND SAMPLE. N^* AND $(V^*)^{1/2}$ ARE THE SMALL SAMPLE ESTIMATES OF POPULATION SIZE AND THE STANDARD DEVIATION OF THAT ESTIMATE RESPECTIVELY. SEE TEXT FOR DETAILS.

SPECIES	YEAR	N_1	N_2	M_2	N^*	$(V^*)^{1/2}$	ESTIMATED EGG POOL	ESTIMATED EGG SURVIVAL
<i>S. merriami</i>	1974	12	32	3	106.25	37.41	217.11	0.4894
	1975	39	92	12	285.15	58.28	354.23	0.8050
	1976	6	24	1	86.50	40.95	200.21	0.4320

($\chi_1^2 = 5.18$; $p = 0.0228$) and 1975 ($\chi_1^2 = 29.94$; $p \leq 0.0001$). There was no significant difference in first year survival in 1976 ($\chi_1^2 = 0.004$; $p > 0.9$).

Results of the attempt to estimate egg survival in *S. merriami* are presented in Table 15. These results must be viewed with caution because of the low number of marked hatchlings from known clutches that were actually recaptured. These are statistically significant differences in these estimates of egg survival among the years of this study ($\chi_2^2 = 96.45$; $p \leq 0.0001$). Egg survival was apparently much greater in 1975 than in either 1974 ($\chi_1^2 = 62.47$; $p \leq 0.0001$) or 1976 ($\chi_1^2 = 122.22$; $p \leq 0.0001$); egg survival estimated for 1974 did not differ significantly from that for 1976 ($\chi_1^2 = 1.20$; $p > 0.27$). Survival from hatching to the following June was estimated for both species as the proportion of hatchlings marked on a particular area in a given year that were captured on that area the following year. These data are summarized in Table 16. There were no significant differences among years in these estimates of hatchlings survival for either the tree lizard ($\chi_2^2 = 0.33$; $p > 0.1$) or the canyon lizard ($\chi_2^2 = 2.68$; $p > 0.1$), and there was no significant difference between these species when data from all years are compared ($\chi_2^2 = 0.74$; $p > 0.1$).

SUMMARY OF SURVIVAL.—Post-hatchling survival was independent of age in both species and in all years of the study. Adult survivorship in *U. ornatus* did not vary significantly among the years of this study, and adult male and female tree lizards did not differ significantly in their annual survival in any year of the study. Male and female tree lizards did not differ in first year survival in any year of the study, but first year survival varied significantly among years. Survival of animals from hatchlings until June of the following year did not vary significantly among years in *U. ornatus*. Thus, the observed variation in first year survival is probably accounted for by variation in egg survival, although it was not possible to measure egg survival in tree lizards.

There were statistically significant differences in annual adult survival between male and female *S. merriami* when data from all years were compared. Adult female canyon lizards experienced higher mortality rates than males in all years. Both sexes suffered significantly higher adult mortality in 1976 than in 1974 or 1975. First year survivorship did not differ significantly between male and female *S. merriami* during this study. First year survival did, however, vary significantly among years. First year survival was dramatically higher in 1975 than in either 1976 or 1977. Survival from hatching to June of the following year did not vary among years in *S. merriami* and the estimate of egg survival was much higher in 1975 than in 1974 and 1976. Apparently the increased first year survival shown by the cohort born in 1975 is attributable to increased egg survival in that year.

First year survival was higher in *S. merriami* than in *U. ornatus*. There was no significant difference between the two in the survival of marked hatchlings; therefore, differences in egg mortality are presumed to be responsible for the differences in first year mortality. Annual adult survival was greater in male *S. merriami* than male *U. ornatus* in 1974 and 1975, but there was no significant difference in 1976. Annual adult survival did not differ between female *S. merriami* and *U. ornatus* in any year. In both species, first year

TABLE 16
ESTIMATES OF MINIMAL HATCHLING SURVIVAL, P_H YEARLINGS OF
MARKED HATCHLINGS. N_1 IS THE NUMBER MARKED AS
HATCHLINGS, N_2 IS THE NUMBER RECAPTURED AS YEARLINGS.
DATA FROM BOTH SEXES WERE POOLED.

SPECIES	YEAR	N_1	N_2	$P_H(S)$
<i>S. merriami</i>	1974	24	7	0.2917
	1975	39	12	0.3077
	1976	43	7	0.1628
	TOTAL	106	26	0.2453
<i>U. ornatus</i>	1974	16	4	0.2500
	1975	27	6	0.2222
	1976	38	7	0.1842
	TOTAL	81	17	0.2099

survivorship was much more variable among years than post-hatchling survival.

INDIVIDUAL GROWTH.—Individual growth rates in both *S. merriami* and *U. ornatus* (and other lizards) are a function of body size (and hence age), season, and the availability of resources. Most growth in these two species occurs in the first year of life, and SVL changes very little thereafter. Individuals of both species grow little, if at all, during the period of inactivity associated with the cold months (November–March). The active season of *S. merriami* and *U. ornatus* are divided into an early period (April–early August) of reproduction followed by a later period (August–October) of growth and lipid accumulation. Sexually mature individuals grow little, if at all, during the period of reproduction, whereas sexually immature individuals grow continually throughout the active season. This pattern is found frequently in other oviparous iguanids such as the side-blotched lizard, *Uta stansburiana* (Tinkle, 1967; Nussbaum and Diller, 1976). Data on body size (SVL) of animals of known age reveal the overall growth patterns of both species and are summarized in Figs. 10-13.

The logistic-by-weight growth models estimated from the recapture data for the populations of *U. ornatus* are presented in Table 17. Separate models were computed for the wet (1974, 1976) and dry (1975, 1977) years of this study. The 95% “support plane” confidence intervals about the point estimate (\hat{A}) of asymptotic body size overlapped in all pairwise comparisons, indicating that the asymptotic body size does not vary significantly between sexes in either the wet or dry years of this study or among wet and dry years independent of sex. There were no significant differences in the estimates of the characteristic growth parameter (r) between the sexes in any year of the study. Thus, these models provide no evidence of significant sexual dimorphism in body size (SVL) in these populations of *U. ornatus*. There were, however, significant differences between the estimates of the characteristic

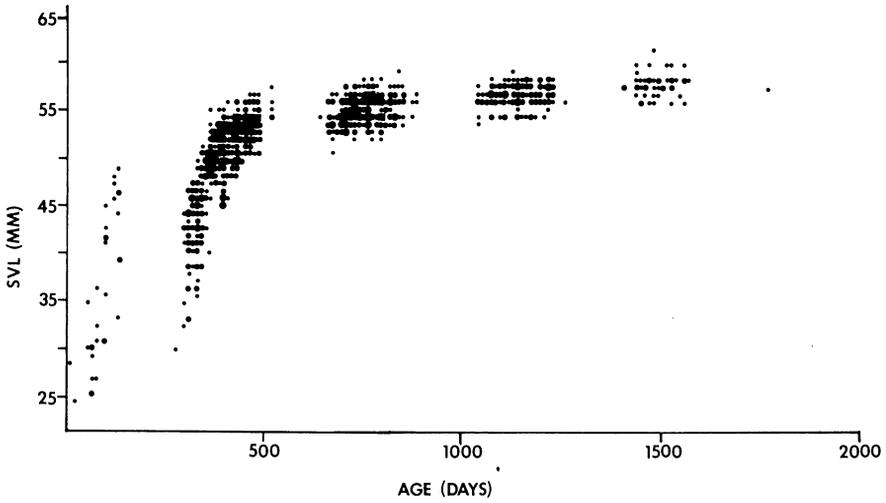


Fig. 10 Body size (SVL) of male *S. merriami* as a function of age. Based on animals of known age.

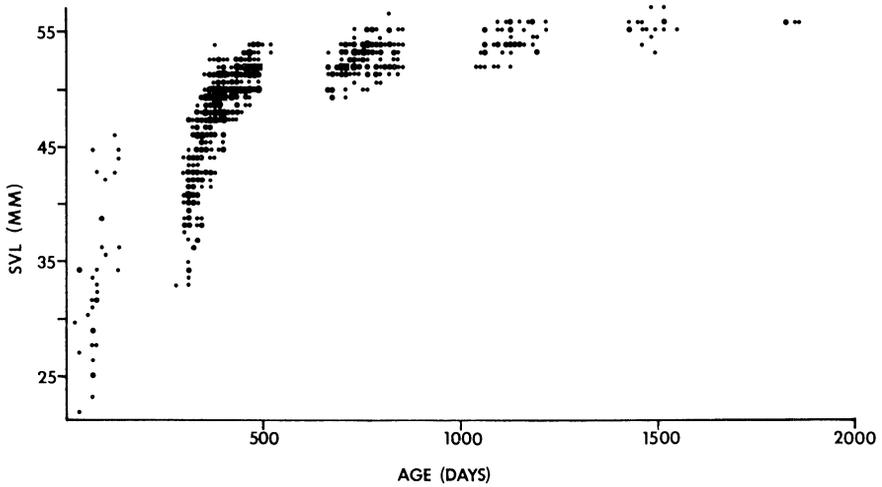


Fig. 11 Body size (SVL) of female *S. merriami* as a function of age. Based on animals of known age.

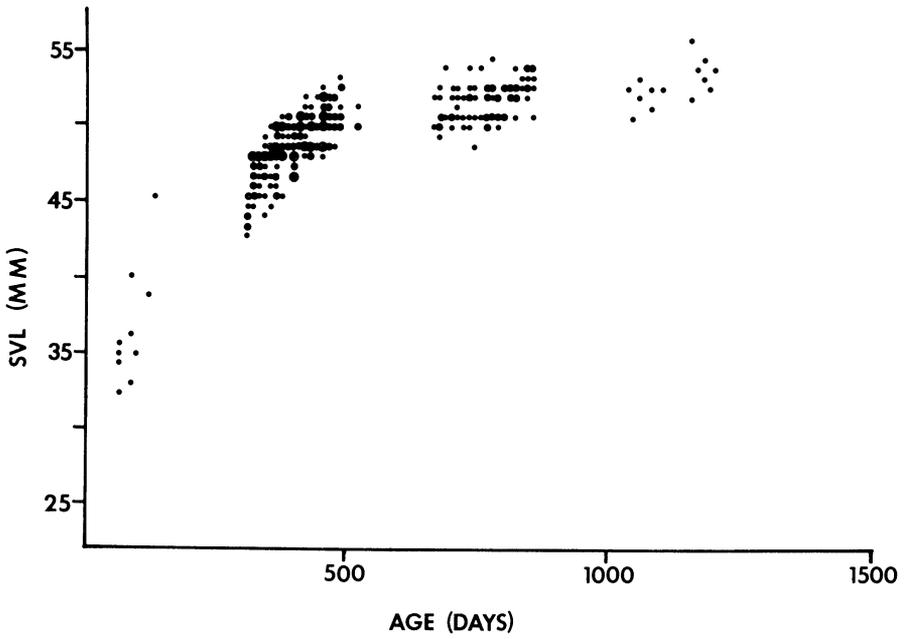


Fig. 12 Body size (SVL) of male *U. ornatus* as a function of age. Based on animals of known age.

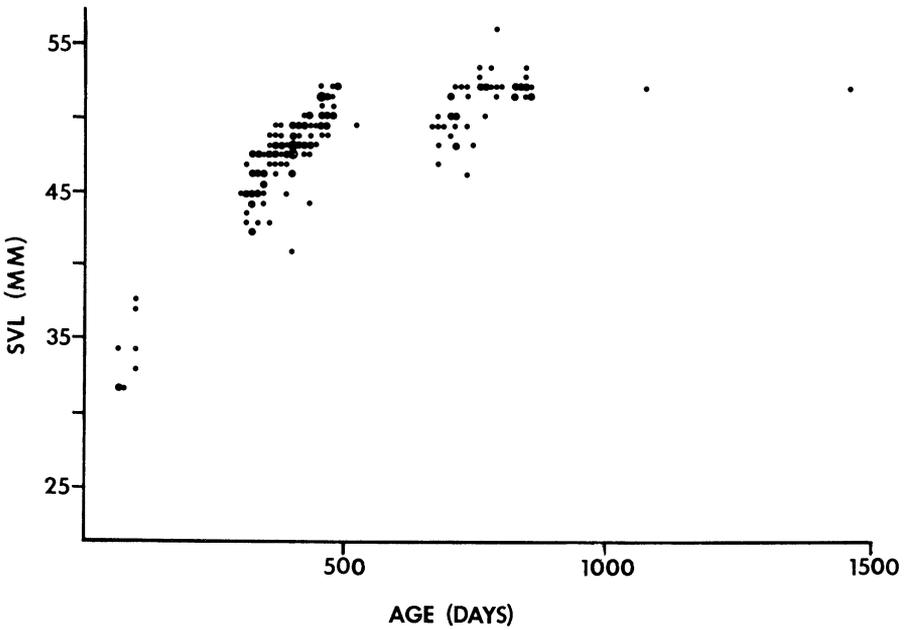


Fig. 13 Body size (SVL) of female *U. ornatus* as a function of age. Based on animals of known age.

TABLE 17
SUMMARY OF ESTIMATED PARAMETERS FOR THE LOGISTIC-BY-WEIGHT MODELS OF INDIVIDUAL GROWTH IN *U. ORNATUS* FOR THE WET (1974, 1976) AND DRY (1975, 1977) YEARS OF THE STUDY. ALSO PRESENTED ARE THE 95% "SUPPORT PLANE" CONFIDENCE INTERVAL HALF WIDTHS FOR EACH PARAMETER ESTIMATE. N IS SAMPLE SIZE, SSQR/N IS THE RESIDUAL ERROR MEAN SQUARE, \hat{A}_l IS THE ASYMPTOTIC BODY SIZE ESTIMATE, AND \hat{r} IS THE ESTIMATE OF CHARACTERISTIC GROWTH RATE.

YEAR	N	SSQR/N	\hat{A}_l	\hat{r}
Males:				
1974, 1976	158	0.8894	50.07 ± 0.41	0.0243 ± 0.0011
1975, 1977	180	0.8435	50.02 ± 0.55	0.0121 ± 0.0008
Females:				
1974, 1976	104	1.2341	49.69 ± 0.78	0.0134 ± 0.0028
1975, 1977	106	1.3304	49.04 ± 0.94	0.0062 ± 0.0011

growth parameter (r) from the data for the wet (1974, 1976) and dry years (1975, 1977) of the study. Tree lizards exhibited lower individual growth rates (r) in the dry years of this study and the response of the two sexes was concordant, as evidenced by lack of significant differences between the models for males and females in any year.

The analysis of individual growth of *S. merriami* (Table 18 and Dunham 1978a) revealed no significant differences among years in the estimates of asymptotic body size (A) for either males or females. However, in each year of the study, the estimated asymptotic SVL of male *S. merriami* was significantly greater than that of females. There was no significant difference between the "characteristic growth rates" (r) of males and females in any year of the study. Males attain a significantly greater asymptotic SVL than females but both sexes approach their respective asymptotic sizes at the same rates (r). Therefore, the absolute growth rates of males must be higher than are those of females. These results were unaltered by subdividing the data by study site and recomputing the models. This pattern was also found by Schoener and Schoener (1978) in several *Anolis* populations. The growth rates (r) of both males and females varied concordantly among the years of this study. The estimates of the characteristic growth rate (r) of both males and females were lower in the dry years (1975, 1977) than in the wet years (1974, 1976). All of these contrasts are statistically significant (Table 18) except that the 95% "support plane" confidence intervals about the esti-

TABLE 18
SUMMARY OF ESTIMATED PARAMETERS OF THE LOGISTIC-BY-WEIGHT
MODELS OF INDIVIDUAL GROWTH OF *S. MERRIAMII* IN THE WET (1974, 1976)
AND DRY (1975, 1977) YEARS OF THIS STUDY. ALSO PRESENTED ARE
THE 95% "SUPPORT PLANE" CONFIDENCE INTERVAL HALF WIDTHS FOR
EACH PARAMETER ESTIMATED. TERMINOLOGY IS AS IN TABLE 17.

YEAR	N	SSQR/N	\hat{A}_l	\hat{r}
Males:				
1974	103	0.0057	56.41 ± 0.63	0.0224 ± 0.0025
1975	102	0.0107	56.70 ± 0.57	0.0208 ± 0.0017
1976	236	0.0046	56.68 ± 0.50	0.0247 ± 0.0015
1977	198	0.0063	56.28 ± 0.54	0.0204 ± 0.0011
Females:				
1974	56	0.0244	53.29 ± 1.38	0.0220 ± 0.0048
1975	56	0.0350	53.52 ± 1.07	0.0200 ± 0.0024
1976	151	0.0101	53.37 ± 0.68	0.0269 ± 0.0022
1977	148	0.0119	53.45 ± 0.94	0.0206 ± 0.0023

mates for r for male and female *S. merriami* in 1974 overlap those for the other three years. The overlap is not great, however, and the 95% "support plane" confidence intervals are very conservative. Standard, single parameter confidence intervals and the 75% error bounds do not overlap.

In order to assay the general body condition of the canyon and tree lizard populations during this study, I computed linear regression models of the relationship of body weight to SVL for males and females of each species residing on the study plots during the period immediately prior to hibernation (September and October). Body weight is related to SVL by a power function; I therefore computed simple linear regression models on logarithmically transformed weights and lengths. These models were tested for statistically significant differences using covariance analysis and, in the absence of significant differences among the models for males or females of each species, were pooled and separate models for wet and dry years computed. The results of this analysis are presented in Table 19. Again the males and females of both species responded concordantly to the differences in conditions between wet (1974, 1976) and dry (1975, 1977) years. In each case, there were significant differences among the regression models with the adjusted mean weight being significantly lower in dry years than in wet years. There were no significant differences among the slopes of the models being contrasted and examination of residuals of each model indicated no major departure from the assumptions of linear regression analysis or covariance analysis.

TABLE 19
 SUMMARY OF THE COVARIANCE AND ANALYSIS COMPARING PREHIBERNATION SIZE-SPECIFIC BODY WEIGHTS IN
S. MERRIAMII AND *U. ORNATUS* IN WET AND DRY YEARS. REGRESSION MODELS ARE OF THE FORM: $\ln Y = a(\ln X) + b$; IN ALL
 MODELS THE COVARIATE IS THE LOGARITHM OF SVL. *** IMPLIES $p \leq 0.0001$; ** IMPLIES $p \leq 0.01$.

SPECIES	SEX	YEARS	F STATISTICS		SLOPES	ADJUSTED MEANS
			a	b		
<i>S. merriami</i>	male	dry	2.88	-10.08	$F_{1,39} = 0.09^{NS}$	$F_{1,40} = 14.50^{***}$
		wet	2.17	-7.03		
	female	dry	2.71	-9.41	$F_{1,27} = 0.01^{NS}$	$F_{1,28} = 34.06^{***}$
		wet	3.00	-10.38		
	male	dry	2.45	- 8.59	$F_{2,18} = 20.20^{***}$	$F_{1,18} = 0.38^{NS}$
		wet	2.57	- 8.92		$F_{1,10} = 41.47^{***}$
female	dry	1.65	- 5.49	$F_{2,17} = 17.23^{**}$	$F_{1,18} = 2.24^{NS}$	
	wet	2.09	- 7.10		$F_{1,17} = 17.23^{**}$	

SUMMARY OF GROWTH AND BODY SIZE VARIATION.—The analysis of individual growth patterns (Tables 17 and 18) indicated significant sexual size dimorphism in *S. merriami* with the asymptotic body size (SVL) of males (about 56 mm) being significantly larger than that of females (about 53 mm). There were no significant differences in the asymptotic body size or characteristic growth rate estimates for male and female *U. ornatus*. The asymptotic SVL of both sexes in the tree lizard is about 50 mm, indicating a lack of significant sexual size dimorphism in these tree lizards. The relationship, if any, of these differences to the fact that male *S. merriami* have higher annual adult survival (see section on survivorship) than females while there is no significant difference between sexes in the average adult survival of tree lizards, remains obscure.

Males and females of both species responded concordantly to the differences between the environmental conditions obtaining in wet years (1974, 1976) and dry years (1975, 1977). Males and females of both species exhibited lower growth rates and lower prehibernation body weight for a given SVL in dry years than in wet years. These results suggest that both species may be limited by the same factors and that growth rates and body weight changes may be sensitive indicators of the environmental conditions (e.g., food availability or the intensity of competition) at any given time in these lizard populations.

INDIVIDUAL FORAGING SUCCESS.—Wet weights of the stomach contents of adult males sacrificed for reproductive data in 1976 and 1977 were summarized by Dunham (1980). There was a significant Spearman rank correlation between the mean weight of food in the stomachs of *S. merriami* and that in the stomachs of *U. ornatus* on comparable sampling dates in both 1976 ($r_s = 0.93$; $0.01 \leq p \leq 0.02$) and 1977 ($r_s = 0.94$; $p \leq 0.01$). There was also a significant correlation between the mean weight of food in the stomachs of *S. merriami* ($r_s = 0.88$; $p \leq 0.05$) and *U. ornatus* ($r_s = 0.83$; $p \leq 0.05$) and the D-Vac[™] estimate of prey abundance in 1976. The mean weights of food in the stomachs of these lizards and the D-Vac[™] estimate of abundance in 1977 were also correlated ($r_s = 0.89$; $p \leq 0.02$ for *U. ornatus* and $r_s = 0.94$; $p \leq 0.01$ for *S. merriami*). The relationship between the mean weight of food in the stomachs of male tree and canyon lizards is summarized in Fig. 14. There was a significant correlation between estimated food abundance and this measure of foraging success in both *U. ornatus* ($r_s = 0.87$; $p \leq 0.02$) and *S. merriami* ($r_s = 0.85$; $p \leq 0.02$) for all sampling dates.

The second method of estimating individual foraging success consisted of direct field observation of foraging males of both species. My assistants and I observed marked lizards on the study plots in 1976. These observations were carried out between 0800 and 1100 CDT, and only data from actively foraging males were used in the analysis. The duration of observation of each lizard was timed with a stopwatch, and the number of feeding strikes made by each animal counted. These data were then converted into a feeding rate. In order to have observations of an adequate number of

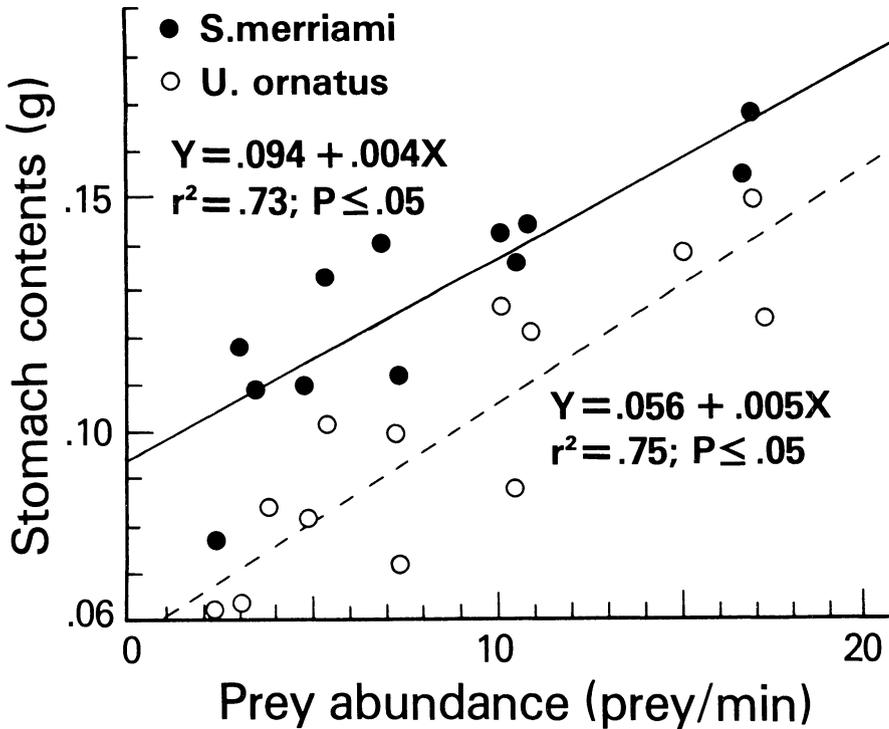


Fig. 14 The relationship between the mean wet weight of stomach contents and the D-Vac[®] estimate of food abundance for adult male *S. merriami* and *U. ornatus*.

lizards, I lumped the data into samples from 3 two-week intervals, late June, early August, and late August (Table 20). The distributions of foraging success on these three dates differed significantly as revealed by pairwise Mann-Whitney U comparisons. Observed feeding rates (Table 20) of both *U. ornatus* ($U = 596.0$; $p \leq 0.0001$) and *S. merriami* ($U = 1363.0$; $p \leq 0.0001$) were lower in late June than in early August. Feeding rates were also significantly lower in late June than in late August in both the tree lizard ($U = 493.0$; $p \leq 0.0001$) and the canyon lizard ($U = 783.0$; $p \leq 0.0001$). Differences in observed foraging rates between early and late August were not statistically significant in *U. ornatus* ($U = 309.5$; $p > 0.10$). Thus, the lower prey abundance in late June (Fig. 3) was reflected in reduced foraging success during that time period in both species.

The final method of estimating individual foraging success involved quantifying prehibernation storage lipid levels and size-specific body weights in males and females of both species in a wet year (1976) and a dry year (1977). Total body lipid was calculated for each animal as the sum of the dry weights of lipids stored in the corpora adiposa, carcass, and liver. These results are presented in Figs. 15 and 16. In males and females of both species, the total

TABLE 20
FORAGING SUCCESS OF ADULT MALE *S. MERRIAMI* AND *U. ORNATUS*
AS MEASURED BY OBSERVED FEEDING RATES DURING LATE JUNE, EARLY
AUGUST, AND LATE AUGUST OF 1976. N IS THE NUMBER OF ANIMALS
OBSERVED. NUMBERS IN PARENTHESES ARE THE 75% ERROR BOUNDS.

SPECIES	DATE	N	FEEDING STRIKES HR ⁻¹
<i>U. ornatus</i>	late June	24	5.47 (0.94)
	early August	25	14.58 (0.98)
	late August	21	14.57 (1.50)
<i>S. merriami</i>	late June	29	6.56 (0.82)
	early August	49	20.33 (0.85)
	late August	27	21.45 (0.81)

prehibernation lipid depends on SVL and this relationship is non-linear. I used the analysis of covariance (ANCOVA) on the logarithmically transformed variables to compare the size-specific prehibernation lipid levels and body weights of animals collected in different years (Tables 21 and 22). In all cases, the size-specific lipid levels and body weights of control animals

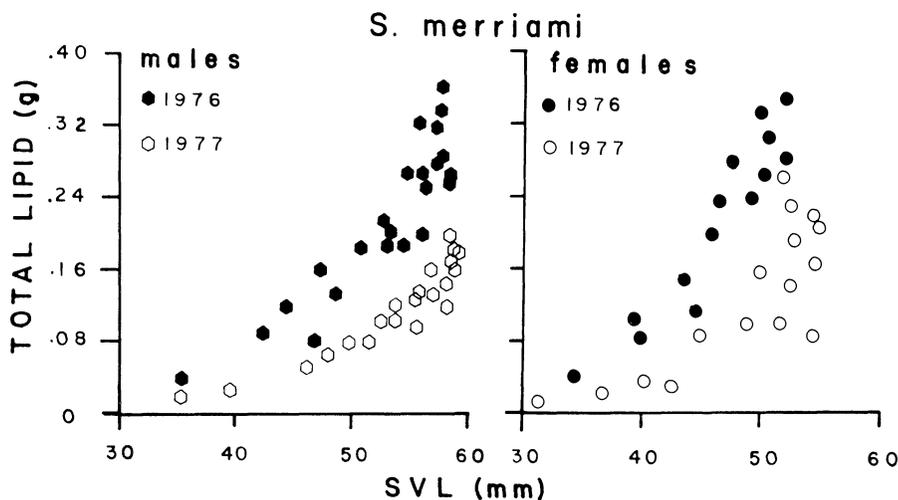


Fig. 15 The relationship between total prehibernation lipid and body size (SVL) in 1976 and 1977 for *S. merriami*.

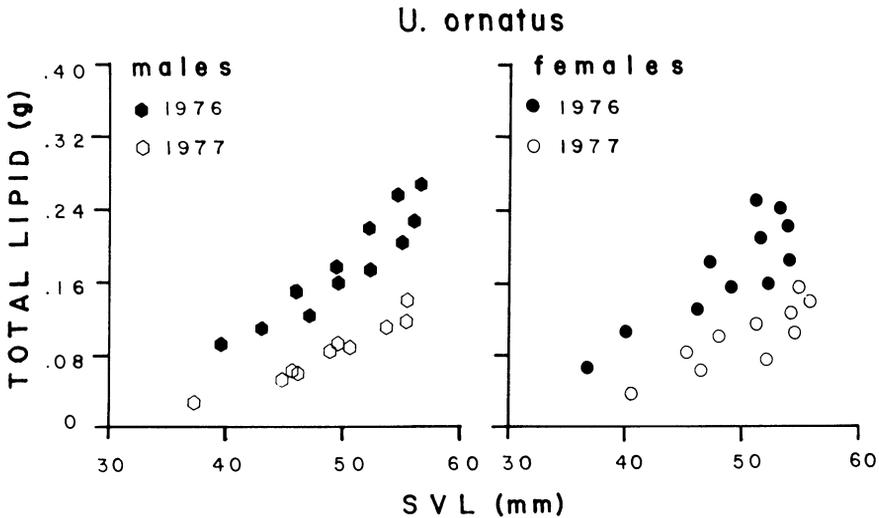


Fig. 16 The relationship between total prehibernation lipid and body size (SVL) in 1976 and 1977 for *U. ornatus*.

collected in the dry (1977) year were significantly lower than those of control animals collected in the wet (1976) year (Table 23). For example, a prehibernation female canyon lizard which was 50 mm SVL in 1976 would be expected to weigh 3.94 g and to have about 0.28 g of stored lipid. In 1977 the predicted wet weight of the same female would be about 3.31 g and the predicted total body lipid would be about 0.12 g, corresponding to a weight difference of 0.63 g (16%) and a difference in stored lipid of 0.16 g (57%). Similar differences were apparent in male *S. merriami* and in both sexes of *U. ornatus* (Table 23).

In addition, covariance analysis revealed that prehibernation male *U. ornatus* were significantly heavier in 1976 ($F_{1,19} = 4.35$; $p > 0.05$) than females of the same SVL, although the slopes of the two regression models were different ($F_{1,19} = 10.13$; $p \leq 0.005$). Size-specific body weights of male and female *U. ornatus* did not differ in the dry year (1977). Likewise, there was no significant difference in total prehibernation body lipid between male and female *U. ornatus* of the same SVL in 1976 ($F_{1,10} = 4.28$; $p > 0.1$). However, in 1977 the total prehibernation lipids were significantly greater

TABLE 21
 SUMMARY OF THE COVARIANCE ANALYSIS COMPARING PREHIBERNATION BODY WEIGHTS AND STORAGE LIPIDS IN
S. MERRIAMII FOR 1976 AND 1977. REGRESSION MODELS ARE OF THE FORM: $\ln Y = a(\ln X) + b$; IN BOTH MODELS THE
 COVARIATE IS THE LOGARITHM OF SVL. *** IMPLIES $p \leq 0.0001$, ** IMPLIES $p \leq 0.01$.
 F STATISTICS

SPECIES (VARIABLE)	SEX	YEAR	a	b	EQUAL REGRESSIONS	EQUAL SLOPES	EQUAL ADJUSTED MEANS
<i>S. merriami</i> (Prehibernation Body Weights)	MALE	1976	2.166	-7.029			
		1977	2.882	-10.076	$F_{2,39} = 9.01^{***}$	$F_{1,39} = 0.09^{NS}$	$F_{1,40} = 14.50^{***}$
	FEMALE	1976	3.004	-10.379			
		1977	2.710	-9.405	$F_{2,27} = 19.11^{***}$	$F_{1,27} = 0.01^{NS}$	$F_{1,28} = 34.06^{***}$
<i>S. merriami</i> (Prehibernation Lipids)	MALE	1976	3.862	-16.880			
		1977	5.048	-22.334	$F_{2,39} = 125.34^{***}$	$F_{1,39} = 9.87^{**}$	$F_{1,40} = 197.09^{***}$
	FEMALE	1976	5.003	-20.841			
		1977	5.122	-22.161	$F_{2,27} = 32.68^{***}$	$F_{1,27} = 0.02^{NS}$	$F_{1,28} = 67.71^{***}$

TABLE 22
 SUMMARY OF THE COVARIANCE ANALYSIS COMPARING PREHIBERNATION BODY WEIGHTS AND STORAGE LIPIDS IN
U. ORNATUS FOR 1976 AND 1977. REGRESSION MODELS ARE OF THE FORM: $\ln Y = a(\ln X) + b$; IN BOTH MODELS THE
 COVARIATE IS THE LOGARITHM OF SVL. *** IMPLIES $p \leq 0.0001$; ** IMPLIES $p \leq 0.01$.

SPECIES (VARIABLES)	SEX	YEAR	a	b	F STATISTICS		
					EQUAL REGRESSIONS	EQUAL SLOPES	EQUAL ADJUSTED MEANS
<i>U. ornatus</i> (Prehibernation Body Weights)	MALE	1976	2.572	- 8.923	$F_{2,18} = 20.20^{***}$	$F_{1,18} = 0.358^{NS}$	$F_{1,19} = 41.47^{***}$
		1977	2.445	- 8.585			
	FEMALE	1976	2.091	- 7.096	$F_{2,17} = 17.23^{**}$	$F_{1,17} = 2.24^{NS}$	$F_{1,18} = 17.23^{**}$
		1977	1.642	- 5.492			
<i>U. ornatus</i> (Prehibernation Lipids)	MALE	1976	2.802	-12.757	$F_{2,18} = 161.28^{***}$	$F_{1,18} = 2.56^{NS}$	$F_{1,19} = 295.70^{***}$
		1977	3.380	-15.757			
	FEMALE	1976	2.742	-12.408	$F_{2,17} = 32.22^{***}$	$F_{1,17} = 0.57^{NS}$	$F_{1,18} = 65.42^{***}$
		1977	3.283	-15.144			

TABLE 23
 REPRESENTATIVE CLUTCH SIZES, PREHIBERNATION BODY WEIGHTS, AND TOTAL PREHIBERNATION BODY LIPIDS OF
 FEMALE *SCELOPORUS MERRIAM* AND *UROSAURUS ORNATUS* AS A FUNCTION OF SVL AND YEAR QUALITY. THESE VALUES
 ARE BASED ON THE ANCOVA MODELS PRESENTED IN TABLES 5, 21, AND 22. % D IS THE PERCENT DIFFERENCE IN THE
 RESPONSE VARIABLE WHEN YEARS ARE CONTRASTED.

Species	SVL	Clutch Size		Body Weight			Total Body Lipids		
		wet	dry	1976	1977	% D	1976	1977	%D
<i>S. merriami</i>	50.0	4.51	4.02	3.88	3.36	13.43	0.300	0.120	60.2
	45.0	3.91	3.19	2.82	2.55	9.52	0.148	0.062	57.6
	40.0	****	****	1.97	1.88	4.95	0.067	0.030	54.7
	30.0	****	****	0.83	0.89	-6.71	0.010	0.005	45.3
<i>U. ornatus</i>	50.0	5.60	4.53	2.91	2.71	6.87	0.171	0.093	45.5
	45.0	4.35	3.33	2.36	2.20	6.78	0.126	0.062	50.5
	40.0	****	****	1.86	1.75	5.91	0.090	0.040	55.6
	30.0	****	****	1.05	0.99	5.18	0.039	0.013	65.8

in females than in males of equal SVL ($F_{1,17} = 12.63$; $p \leq 0.002$), and the slopes of the regression models did not differ significantly ($F_{1,16} = 0.02$; $p > 0.8$).

Covariance analysis of size-specific body weights of prehibernation *S. merriami* revealed that in 1976 males and females did not differ significantly ($F_{1,34} = 19.50$; $p > 0.1$). Regression models relating the logarithm of body weight to the logarithm of SVL did not differ ($F_{2,33} = 2.24$; $p > 0.1$). The same result was obtained in the analysis of the data from 1977 ($F_{1,34} = 0.03$; $p > 0.8$ for adjusted means; $F_{2,33} = 0.55$; $p > 0.5$ for regressions). Comparison of prehibernation lipid levels in male and female *S. merriami* revealed highly significant differences in both 1976 ($F_{1,34} = 42.03$; $p \leq 0.0001$) and 1977 ($F_{1,34} = 27.82$; $p \leq 0.0001$). Female canyon lizards had higher size-specific lipid levels in both years. There was a significant difference in the slopes of the regression models in 1976 ($F_{1,22} = 4.98$; $p \leq 0.03$) but not in 1977 ($F_{1,33} = 0.02$; $p > 0.8$).

Data presented in this section strongly indicate that individual foraging success is related to arthropod abundance in both species. The most convincing data are those on prehibernation lipid levels and body weights. Males and females of both species exhibited significantly (ANCOVA) lower size-specific prehibernation lipid levels and body weights in the dry year (1977). The comparison of the sticky trap estimates of arthropod abundance presented previously indicated that there was significantly less food available to saxicolous insectivores such as *S. merriami* and *U. ornatus* in 1977. The prehibernation body weight and lipid level data strongly suggest that these lizards were less successful in harvesting food resources in 1977 than in 1976.

SUMMARY AND DISCUSSION

This study demonstrates significant yearly and seasonal variation in several phenotypic attributes of importance to the Darwinian fitness of the individuals of *Sceloporus merriami* and *Urosaurus ornatus* from the populations studied. Age-specific survival, age-specific fecundity, age-specific body size and growth rate, individual foraging success, and prehibernation lipid levels and body weights were all shown to vary significantly, both seasonally and among years in both species. This variation is explained by seasonal and annual variation in the arthropod prey of these two species, and prey abundance was shown to vary as a function of the amount of precipitation.

A number of investigators have hypothesized a positive relationship between precipitation and food availability for lizards inhabiting arid or semi-arid regions of North America. Most have related this pattern to reproductive success (Hoddenbach and Turner, 1968; Martin, 1977; Mayhew, 1965, 1967; Parker and Pianka, 1975; Pianka, 1970; Turner et al., 1970). Mayhew

(1965) stated that the reproductive success of *Uma inornata* is correlated with the previous winter's rainfall. Zweifel and Lowe (1966) indicated that *Xantusia vigilis* produce no young in exceptionally dry years. Increased clutch size correlated with higher rainfall has been reported for *Uta stansburiana* (Hoddenbach and Turner, 1968), *Cnemidophorus tigris* (Pianka, 1970), *Uma scoparia* (Mayhew, 1966), and *Sceloporus virgatus* (Vinegar, 1975). Smith (1977) demonstrated that individual growth rates of striped plateau lizards, *Sceloporus virgatus* and *U. ornatus*, in the Chiricahua Mountains of southeastern Arizona were significantly lower during a drought period than during more favorable periods. Ballinger (1977) demonstrated a positive correlation between rainfall and food resources. In addition, he demonstrated a positive relationship between these and several reproductive parameters of the tree lizards, *Urosaurus ornatus*, in the Animas Mountains of southwestern New Mexico. He also presented data which suggest that individual growth rates may be lower in years characterized by reduced food abundance. Medica, et al. (1975) demonstrated increased individual growth rate in the desert tortoise (*Gopherus agassizi*) following winters of higher precipitation in Nevada, presumably in response to increased primary productivity. These results are consistent with the hypothesis that individual growth rates reflect food abundance in natural populations.

Andrews (1976) and Schoener and Schoener (1978) have shown differences in individual growth rates among populations of *Anolis* which are consistent with the hypothesis that growth rates in these lizards are positively correlated with food abundance. However, food abundance was not measured in any of these studies. Licht (1974) found an increase in lean growth of *Anolis cristatellus* in response to food supplementation in nature.

The data presented here indicate that both seasonal and annual variation in arthropod abundance at the localities studied are serially correlated with variation in the amount of precipitation. Further, significant seasonal and annual variation in arthropod abundance and, hence, in the food resources available to insectivorous lizards such as those studied here is demonstrated. The comparison of sticky trap estimates of arthropod abundance for 1975, 1976 and 1977 demonstrates that on any sampling date the arthropod abundance was greater in 1976. These differences were correlated with differences between these years with regard to the amount and distribution of precipitation.

Individual lizards might be expected to respond in two different ways when a dry year or other factors result in low prey abundance and, hence, in a high resource demand/supply ratio. The first response would be an increase in foraging effort (e.g., time spent foraging) which would be accompanied by a higher cost of resource acquisition. This would most likely be expressed as higher mortality rates due to greater exposure to predation. In this case we would expect to see little, if any, reduction in size-specific body weight or lipid storage. The other potential response to high resource

demand/supply ratios would be to maintain constant (or even reduce) foraging effort which would result in no change (or perhaps reduced) mortality rates. In this case we expect a decrease in size-specific body weight and lipid stores. The data presented here argue that *S. merriami* and *U. ornatus* reacted to the high resource demand/supply ratios which occurred in 1975 and 1977 with the second response. There was no significant difference among years in post-hatchling survival in either species. Size specific body weights and total body lipids of prehibernation lizards of both species were reduced in the dry year (1977). Individuals of both species seemed less active (fewer animals captured per man-hr of censusing effort) during times of reduced food abundance. Although anecdotal, this is also consistent with the second response.

The correlation of the weight of stomach contents from adult *S. merriami* and *U. ornatus* with estimates of food abundance indicates that successful foraging by these animals is dependent, at least in part, on food availability. The effects of this variation among years in precipitation and, hence, in food resource abundance are summarized in Table 24.

To facilitate comparison of *U. ornatus* and *S. merriami*, I have constructed life tables for the Grapevine Hills populations. These are presented in Tables 25 and 26 and are based on the data for the study populations. These life tables are based on data from all years and on the growth trajectories predicted by the logistic-by-weight growth model for females. These life tables do not describe the history of an actual cohort as age-specific fecundity and survival vary significantly among years in both species. The average number of female offspring per female of age x (m_x) in both tables are based on the assumption that the sex ratio in eggs is 1:1. Females were assumed sexually mature if larger than 41 mm for tree lizards and 44 mm for canyon lizards. Size-specific fecundity was computed from regression models (Table 5) predicting clutch size from SVL for first and later clutches. Annual survivorship was assumed constant in animals older than age 1, as indicated by the data on age-specific survival. Life tables were computed to age 15 to avoid the effects of artificial truncation.

The results of this study have shown the canyon lizard and the tree lizard populations in the Grapevine Hills to be remarkably similar in life history and population dynamics, as well as in their response to environmental variation. Both of these populations belong to the short-lived, early-maturing, multiple-clutch subset of lizards as defined by Tinkle et al. (1970). In both species adult survivorship is high and relatively insensitive to environmental variation of the kind and magnitude that occurred during the four years of this study. Both species hatch at about the same SVL and both reach sexual maturity in about 10-12 months. The greater contribution to lifetime reproductive success ($\sum l_x m_x$) is in offspring produced in the second year in both species. Cohort generation time ($1/R_0 \sum [x l_x m_x]$) is slightly greater in *S. merriami* (1.56) than in *U. ornatus* (1.54), and the difference is

TABLE 24
 SUMMARY OF THE EFFECTS OF LOWER FOOD AVAILABILITY IN DRY
 YEARS ON SELECTED LIFE HISTORY CHARACTERISTICS OF
U. ORNATUS AND *S. MERRIAMI*.

Effects of dry years (1975, 1977) on	<i>Urosaurus ornatus</i>	<i>Sceloporus merriami</i>
Individual foraging success	lower	lower
Individual growth rates	lower	lower
Size-specific fecundity of females	lower	lower
Survival of		
Eggs	higher	higher
Hatchlings	no effect	no effect
Adults	no effect	no effect
Size-specific body weight (Prehibernation)	lower	lower
Size-specific Prehibernation Lipid Storage	lower	lower
Population density (early June)	lower	lower
Age Structure	excess of animals over 2 yrs old	excess of animals over 2 yrs old

probably insignificant. Reproductive value, the age-specific expectation of future offspring, rises rapidly at age one and thereafter undergoes a cyclical fluctuation with age in both species. This is because an individual alive at the beginning of a reproductive season has a much greater probability of living to the next reproductive opportunity (clutch II) than does an individual alive at the end of a reproductive season. As is inevitable when mortality and fecundity schedules are constant (Hamilton, 1966) and as assumed here,

TABLE 25
 LIFE TABLE FOR CONTROL *SCELOPORUS MERRIAMII* POPULATIONS BASED ON THE DATA FROM 1974 - 1977. TERMINOLOGY
 FOLLOWS MERTZ (1971) AND WILBUR (1975); SYMBOLS ARE DEFINED IN TABLE 27. $R_0 = 1.16871$; COHORT GENERATION
 TIME IS 1.5613 YEARS; $\sum_x l_x m_x = 1.82468$.

x	Q_x	l_x	m_x	$l_x m_x$	$x l_x m_x$	F_x	G_x	V_x
0.0000	0.5169	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
0.0822	0.3707	0.5169	0.0000	0.0000	0.0000	0.0000	0.0000	1.9509
1.0000	0.8817	0.1916	1.9890	0.3811	0.3811	0.3261	0.3442	5.7784
1.1671	0.3311	0.1689	2.3588	0.3985	0.4651	0.3410	0.3538	4.3716
2.0000	0.8873	0.0559	2.4991	0.1398	0.2796	0.1196	0.1140	6.6176
2.1671	0.3674	0.0496	2.4988	0.1240	0.2688	0.1061	0.0995	4.7212
3.0000	0.8901	0.0182	2.5609	0.0467	0.1401	0.0400	0.0344	6.5846
3.1671	0.3849	0.0162	2.5622	0.0416	0.1317	0.0356	0.0301	4.5982
4.0000	0.8607	0.0063	2.6503	0.0166	0.0662	0.0142	0.0110	5.7580
4.1671	0.1937	0.0054	2.6261	0.0141	0.0588	0.0121	0.0092	3.6726
5.0000	0.8607	0.0010	2.7412	0.0029	0.0143	0.0024	0.0017	5.8812
5.1671	0.1937	0.0009	2.6582	0.0024	0.0123	0.0020	0.0014	3.7108
6.0000	0.8607	0.0002	2.7412	0.0005	0.0029	0.0004	0.0003	5.9154
6.1671	0.1937	0.0002	2.6904	0.0004	0.0025	0.0003	0.0002	3.7513
7.0000	0.8607	0.0000	2.7872	0.0001	0.0006	0.0001	0.0000	5.9619
7.1671	0.1937	0.0000	2.6904	0.0001	0.0005	0.0001	0.0000	3.7519
8.0000	0.8607	0.0000	2.7872	0.0000	0.0000	0.0000	0.0000	5.9653
8.1671	0.1937	0.0000	2.6904	0.0000	0.0001	0.0000	0.0000	3.7559
9.0000	0.8607	0.0000	2.7872	0.0000	0.0000	0.0000	0.0000	5.9875
9.1671	0.1937	0.0000	2.6904	0.0000	0.0000	0.0000	0.0000	3.7821
10.0000	0.8607	0.0000	2.8803	0.0000	0.0000	0.0000	0.0000	6.1354

TABLE 26

LIFE TABLE FOR CONTROL *UROSAURUS ORNATUS* POPULATIONS BASED ON THE DATA FROM 1974 - 1977. TERMINOLOGY FOLLOWS MERTZ (1971) AND WILBUR (1975); SYMBOLS ARE DEFINED IN TABLE 27. $R_0 = 1.06366$; COHORT GENERATION TIME IS 1.5371 YEARS; $\sum_x l_x m_x = 1.63495$.

x	Q_x	L_x	m_x	$l_x m_x$	$x l_x m_x$	F_x	G_x	V_x
0.0000	0.9281	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
0.0822	0.9226	0.9281	0.0000	0.0000	0.0000	0.0000	0.0000	1.0809
0.1644	0.1469	0.8563	0.0000	0.0000	0.0000	0.0000	0.0000	1.1755
1.0000	0.9401	0.1258	1.5000	0.1887	0.1887	0.1774	0.1812	8.2771
1.0882	0.9363	0.1183	2.2817	0.2699	0.2920	0.2537	0.2583	7.2328
1.1644	0.3084	0.1107	2.3733	0.2628	0.3060	0.2471	0.2507	5.3055
2.0000	0.9401	0.0341	2.4913	0.0851	0.1702	0.0800	0.0785	9.8345
2.0822	0.9363	0.0321	2.5391	0.0815	0.1698	0.0767	0.0749	7.8369
2.1644	0.3084	0.0301	2.5874	0.0778	0.1684	0.0731	0.0712	5.6771
3.0000	0.9401	0.0093	2.6361	0.0244	0.0733	0.0230	0.0216	10.3626
3.0822	0.9363	0.0087	2.6853	0.0234	0.0722	0.0220	0.0207	8.2461
3.1644	0.3084	0.0082	2.7348	0.0223	0.0706	0.0210	0.0196	5.9589
4.0000	0.9401	0.0025	2.7848	0.0070	0.0280	0.0066	0.0060	10.8135
4.0822	0.9363	0.0024	2.8352	0.0067	0.0274	0.0063	0.0057	8.5686
4.1644	0.3084	0.0022	2.8352	0.0063	0.0262	0.0059	0.0053	6.1438
5.0000	0.9401	0.0007	2.8352	0.0019	0.0097	0.0018	0.0016	11.0968
5.0822	0.9363	0.0006	2.9374	0.0019	0.0096	0.0018	0.0015	8.8171
5.1644	0.3084	0.0006	2.9374	0.0018	0.0091	0.0017	0.0014	6.3008
6.0000	0.9401	0.0002	2.9374	0.0005	0.0033	0.0005	0.0004	11.2804
6.0822	0.9363	0.0002	2.9374	0.0005	0.0031	0.0005	0.0004	8.9040
6.1644	0.3084	0.0002	2.9374	0.0005	0.0030	0.0005	0.0004	6.3937
7.0000	0.9401	0.0001	3.0412	0.0001	0.0011	0.0001	0.0001	11.5923
7.0822	0.9363	0.0001	3.0412	0.0001	0.0010	0.0001	0.0001	9.1260
7.1644	0.3084	0.0000	3.0412	0.0001	0.0010	0.0001	0.0001	6.5206
8.0000	0.9401	0.0000	3.0412	0.0000	0.0003	0.0000	0.0000	11.6695
8.0822	0.9363	0.0000	3.0412	0.0000	0.0003	0.0000	0.0000	9.2085
8.1644	0.3084	0.0000	3.0412	0.0000	0.0003	0.0000	0.0000	6.6088
9.0000	0.9401	0.0000	3.1467	0.0000	0.0001	0.0000	0.0000	11.9653
9.0822	0.9363	0.0000	3.1467	0.0000	0.0001	0.0000	0.0000	9.4116
9.1644	0.3084	0.0000	3.1467	0.0000	0.0001	0.0000	0.0000	6.7135
10.0000	0.9401	0.0000	3.1467	0.0000	0.0000	0.0000	0.0000	11.9626

TABLE 27
DEFINITIONS OF LIFE TABLE FUNCTIONS.

Q_x	The probability that an individual of age x will survive to age $x + 1$.
l_x	The probability that an individual of age 0 will survive to age x . $l_x = \prod_x Q_x$.
m_x	The number of female offspring produced by a female in the interval $(x - \frac{1}{2})$ to $(x + \frac{1}{2})$.
R_0	The net replacement rate per generation. $R_0 = \sum l_x m_x$.
T_c	The cohort generation time. $T_c = (1/R_0) \sum x l_x m_x$.
F_x	The probability density function for the ages at which a female's daughters are produced. $F_x = (l_x m_x)/R_0$.
G_x	The probability density function for the ages at which mothers actually give birth. $G_x = l_x m_x \exp(-rx)$.
V_x	The reproductive value of a female of age x . $V_x = (1/l_x) \sum_{y=x} l_y m_y \exp[r(x-y)]$.
r	The ultimate rate of increase implicitly defined by the equation. $1 = \sum l_x m_x \exp(-rx)$.

there is no tendency for reproductive value to decrease systematically with age in either life table. However, if senescence occurs in these lizards, as is almost certain, reproductive value would decline after a certain age.

The differences among years in recruitment to these populations are largely accounted for by fluctuation in egg survival between years. The fact that egg survival was much higher in 1975 than 1974 or 1976 is surprising. Blair (1960) reported that the most important source of mortality in undisturbed nests of *Sceloporus olivaceous* was desiccation. The sources of egg mortality in these populations are unknown, but the dramatically increased survival in the dry year argues that it is not desiccation. Of the numerous gaps in our knowledge of the magnitude and sources of variation in the life history characteristics and population dynamics of lizards, the most glaring is our lack of solid comparative data on the sources and magnitude of egg mortality.

Adult female tree lizards normally produce three clutches per year in the Grapevine Hills populations and canyon lizards produce two. The mean clutch size of *U. ornatus* was 4.70 ± 0.03 (95%CI) and that of *S. merriami* was 4.51 ± 0.03 . The mean annual egg production was 14.11 eggs in the tree lizard and 9.02 eggs in the canyon lizard. These data combined with those on mean dry egg weight (Table 8) indicate that female tree lizards produce an average of .8559 g (dry weight) of eggs per year, and canyon lizards produce an average of .8821 g.

The similarity in the life histories and population dynamics is surprising given the variation within sceloporine lizards (Tinkle, et al., 1970). The life history characteristics and population dynamics of population of *U. ornatus* from the Grapevine Hills are more similar to those of the syntopic population of canyon lizards than to populations of *U. ornatus* from different parts of the geographic range. Smith (1977) found that *U. ornatus* from the Chiricahua Mountains of southeastern Arizona mature in their first year,

exhibit high annual adult survivorship (about 0.56) and may lay as many as two clutches per year, although most of the annual reproduction is concentrated in a larger (about 10 eggs) clutch produced late in the year (July). In favorable years two clutches are produced by the larger females. The second clutch, when produced, is smaller (about 5 eggs) and produced in August. The mean generation time is about 2.24 years. The *Urosaurus* populations studied by Ballinger (1977) in the Animas Mountains of southwestern New Mexico exhibit lower annual adult survivorship (about 0.28), two clutches per year in favorable years, reduction in average clutch frequency in dry years, and clutch size characteristics similar to those (about 10 eggs in the first clutch and 7-9 in the second) of the tree lizard populations studied by Smith (1977). Clutch size increases more rapidly with SVL in these populations than in the population from the Grapevine Hills.

No other studies of life history characteristics or population dynamics of *S. merriami* have been done so the geographic variation of these cannot be assessed. I will compare the life history characteristics of the canyon lizard population from the Grapevine Hills to *Sceloporus undulatus consobrinus* in southwestern New Mexico (Vinegar, 1975) and to *Sceloporus virgatus* in southeastern Arizona (Smith, 1977).

Female *S. u. consobrinus* from the population studied by Vinegar (1975) reach an average adult SVL of about 68 mm, mature in their first year (at about 11-14 months), lay four or more clutches of 9-10 eggs between May and July each year and exhibit low annual adult survivorship (about 0.21).

Female *S. virgatus* from the population studied by Smith (1977) average about 62 mm SVL, concentrate their annual reproduction in a single, large (about 10 eggs) clutch produced late in the year and coincident with the advent of the annual wet season, exhibit high annual adult survivorship (about 0.78), delay reproduction until their second year, and have a mean generation time of about 2.91 years.

Against this comparison, the life history characteristics and dynamics of the populations of *U. ornatus* and *S. merriami* from the Grapevine Hills are surprisingly similar. This similarity suggests that these two populations are limited by similar, if not the same, factors. The concordant response of these two populations to variation in resource abundance suggests the same thing and implicates prey abundance as a limiting factor in dry years.

The results of this study have shown that seasonal and annual variation in the amount of precipitation results in predictable variation in the availability of arthropod prey to these lizards which, in turn, results in variation in individual foraging success, growth rates, size-specific fecundity and pre-hibernation lipid levels. Specifically, in years of low rainfall and reduced prey availability, individuals exhibit lowered size-specific fecundity, growth rates, and pre-hibernation lipid levels. This suggests that if these species compete for food, the intensity of that competition is not constant and should be more severe in years characterized by low rainfall and reduced

prey abundance. The experimental study of competition between these two species reported elsewhere (Dunham, 1978b, 1980) revealed this to be the case.

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LITERATURE CITED

- Andrews, R.M. 1976. Growth rate in island and mainland anoline lizards. *Copeia* 1976:477-482.
- Andrews, R.M., and A.S. Rand. 1974. Reproductive effort in anoline lizards. *Ecology* 55:1317-1327.
- Asplund, K.K. 1964. Seasonal variation in the diet of *Urosaurus ornatus* in a riparian community. *Herpetologica* 20:91-94.
- Asplund, K.K. and C.H. Lowe. 1964. Reproductive cycles of the iguanid lizards *Urosaurus ornatus* and *Uta stansburiana* in southeastern Arizona. *J. Morph.* 115:27-34.

- Ballinger, R.E. 1973. Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology* 54:269-283.
- _____ 1976. Evolution of life history strategies: implications of recruitment in a lizard population following density manipulations. *Southwest. Natur.* 21:203-208.
- _____ 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 59:628-635.
- _____ 1980. Intraspecific variation in demography and life history of the lizard *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology* 60:901-909.
- Blair, W.F. 1960. The rusty lizard. A population study. Univ. Texas Press, Austin. 182p.
- Carpenter, C.C. 1961. Patterns of social behavior of Merriam's canyon lizard (*Sceloporus m. merriami* - Iguanidae). *Southwest. Natur.* 6:138-148.
- Carpenter, C.C. and G. Grubitz, III. 1960. Dominance shifts in the tree lizard (*Urosaurus ornatus* - Iguanidae). *Southwest. Natur.* 5:123-128.
- _____ 1961. Time-motion study of a lizard. *Ecology* 42:199-200.
- Chaney, A.H., and R.E. Gordon. 1954. Notes on a population of *Sceloporus merriami merriami* Stejneger. *Texas J. Sci.* 6:78-82.
- Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological census. *Univ. Calif. Publ. Stat.* 1:131-160.
- Conant, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., Boston.
- Conover, W.J. 1971. Practical nonparametric statistics. John Wiley and Sons, Inc., New York.
- Denyes, H.A. 1956. Natural terrestrial communities of Brewster Co., Texas with special reference to the distribution of the mammals. *Amer. Midl. Natur.* 55:289-320.
- Draper, N.R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York.
- Dunham, A.E. 1978a. Food availability as a proximate factor in influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* 59:770-778.
- _____ 1978b. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Ph.D. Thesis, Univ. of Mich. 249. p.
- _____ 1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. *Ecological Monographs* 50:304-330.
- Hoddenbach, G.A., and F.B. Turner. 1968. Clutch size of the lizard *Uta stansburiana* in southern Nevada. *Amer. Midl. Natur.* 80:262-265.
- Licht, P. 1974. Responses of *Anolis* lizards to food supplementation in nature. *Copeia* 1974:215-221.
- Marquardt, D.W. 1964. Least squares estimation of non-linear parameters. Share distribution No. 3094. Harvard Univ. Computing Center Library.
- Martin, R.F. 1973. Reproduction in the tree lizard (*Urosaurus ornatus*) in central Texas: drought conditions. *Herpetologica* 29:27-32.
- _____ 1977. Variation in the reproductive productivity of range margin tree lizards (*Urosaurus ornatus*). *Copeia* 1977:83-92.
- Mayhew, W.W. 1965. Reproduction in the sand dwelling lizard *Uma inornata*. *Herpetologica* 21:39-55.
- _____ 1967. Comparative reproduction in three species of the genus *Uma*. In W.W. Milstead, (ed.), *Lizard ecology, a symposium*, pp. 45-65. Univ. Missouri Press, Columbia.
- Medica, P.A., R.B. Bury, and F.B. Turner. 1975. Growth of the desert tortoise (*Gopherus agassizi*) in Nevada. *Copeia* 1975:693-643.
- Mertz, D.B. 1971. Life history phenomena in increasing and decreasing populations. In G.P. Patil, E.C. Pielou, and W.E. Waters, (eds.), *Symposium on statistical ecology*, pp. 361-400. Penn State Univ. Press.

- Michel, L. 1976. Reproduction in a southwestern New Mexican population of *Urosaurus ornatus*. Southwest. Natur. 21:281-299.
- Milstead, W.W. 1961. Competitive relations in lizard populations. In W.F. Blair, (ed.), Vertebrate speciation. Univ. Texas Press, Austin.
- _____. 1970. Late summer behavior of the lizards *Sceloporus merriami* and *Urosaurus ornatus* in the field. Herpetologica 26:243-254.
- Muller, C.H. 1937. Vegetation in the Chisos Mountains, Texas. Trans. Texas Acad. Sci. 20:5-31.
- Nussbaum, R.A., and L.V. Diller. 1976. The life history of the side-blotched lizard, *Uta stansburiana* Baird and Girard, in north-central Oregon. Northwest Sci. 50:243-260.
- Olson, R.E. 1973. Variation in the canyon lizard *Sceloporus merriami* Stejneger. Herpetologica 29:116-127.
- Parker, W.S., and E.R. Pianka. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. Copeia 1975:615-632.
- Pianka, E.R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703-720.
- Purdue, J.R., and C.C. Carpenter. 1972. A comparative study of the display motion in the iguanid genera *Sceloporus*, *Uta*, and *Urosaurus*. Herpetologica 28: 137-141.
- Schoener, T.W., and A. Schoener. 1978. Estimating and interpreting body size growth in some *Anolis* lizards. Copeia 1978:390-405.
- Seber, G.A.F. 1973. The estimation of animal abundance and related parameters. Griffin, London. 506p.
- Shelby, S.M. 1965. Standard Math Tables. Fourteenth ed. Chemical Rubber Co.
- Simon, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology 56:993-998.
- Smith, D.C. 1977. Interspecific competition and the demography of two lizards. Ph.D. Thesis, Univ. of Mich. 426p.
- Stebbins, R.C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston. 279p.
- Tinkle, D.W. 1967. The life and demography of the side-blotched lizard. Misc. Publ. Mus. Zool. Univ. of Mich. 132:1-182.
- Tinkle, D.W., and R.E. Ballinger. 1972. *Sceloporus undulatus*: a study of the interspecific comparative demography of a lizard. Ecology 53:570-584.
- Tinkle, D.W., H.M. Wilbur, and S.G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55-74.
- Turner, F.B., G.A. Hoddenbach, P.A. Medica, and J.R. Lannom. 1970. The demography of the lizard, *Uta stansburiana* Baird and Girard, in southern Nevada. J. Anim. Ecol. 39:505-519.
- VanDevender, R.W. 1975. The comparative demography of two local populations of the tropical lizard *Basiliscus basiliscus*. Ph.D. Thesis, Univ. of Mich. 110p.
- Van Loben Sels, R.C. 1976. Reproductive biology of the iguanid lizard *Urosaurus ornatus* in a riparian habitat. M.S. Thesis, Arizona State Univ. 105p.
- Vinegar, M.B. 1972. Evolution of life history phenomena in three forms of the lizard genus *Sceloporus*. Ph.D. Thesis, Univ. of Mich. 114p.
- _____. 1975. Demography of the striped plateau lizard, *Sceloporus virgatus*. Ecology 56:172-182.
- Vitt, L.J. 1974. Winter aggregations, size classes, and relative tail breaks in the tree lizards, *Urosaurus ornatus* (Sauria; Iguanidae). Herpetologica 30:182-183.
- Wauer, R. 1971. Ecological distribution of the birds of the Chisos Mountains, Texas. Southwest. Natur. 16:1-30.
- Wilbur, H.M. 1975. The evolutionary and mathematical demography of the turtle *Chrysemys picta*. Ecology 56:64-77.

- Worthington, R.D., and M.D. Sabath. 1966. Winter aggregations of the lizard (*Urosaurus ornatus ornatus* Baird and Girard) in Texas. *Herpetologica* 22:94-96.
- Zweifel, R.G., and C.H. Lowe. 1966. The ecology of a population of *Xantusia vigilis*, the desert night lizard. *Novit. Amer. Mus. Nat. Hist.* 2247:1-57.

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