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Sceloporus Merriami and *Urosaurus Ornatus*

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AN EXPERIMENTAL STUDY OF INTERSPECIFIC COMPETITION BETWEEN THE IGUANID LIZARDS *SCeloporus* *MERRIAMI* AND *UROSAURUS ORNATUS*¹

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Abstract. Competition between the insectivorous iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus* was studied in a density manipulation experiment conducted in the Grapevine Hills of Big Bend National Park, Texas, USA from 1974 through 1977. Resident lizards were individually marked and censused using standard recapture techniques on six experimental plots chosen for similarity in size, habitat, isolation from one another by habitat unsuitable for these lizards, and initial densities of these two species. All *S. merriami* were removed from two plots, all *U. ornatus* from two, and two plots functioned as controls.

Recaptures of marked individuals provided data on individual growth, age-specific survivorship, size-specific fecundity, and population density. Animals collected near the study plots provided data on size-specific fecundity, individual foraging success, and total prehibernation lipid levels. Observations of marked individuals provided estimates of individual foraging success.

Rainfall varied dramatically during the 4 yr of the study; in 1974 and 1976 precipitation was much greater than the 22-yr average, and in 1975 and 1977 precipitation was much less than average. Two methods of estimating arthropod abundance indicated that significantly fewer prey were available to these lizards in the dry years. Individual foraging success, growth rates, body masses, prehibernation lipid levels, and population densities were significantly lower in the control populations of both species in 1975 and 1977 than in 1974 or 1976, indicating that individuals of both species experienced stressful conditions during the dry years.

The removal of *S. merriami* resulted in significant effects on experimental populations of *U. ornatus* only during 1975 and 1977. The density of *U. ornatus* on the experimental plots increased significantly after the removal of *S. merriami*, even though the control populations declined. Individual foraging success, growth rate, prehibernation body mass, and lipid levels were significantly greater in *U. ornatus* from experimental populations than in those from control populations in the dry years of the study. The two treatments did not differ significantly in the wet years. Experimental populations of *S. merriami* exhibited significantly higher adult and juvenile survival than did the control populations in 1975. This was the only significant treatment effect demonstrable in experimental populations of *S. merriami*.

Experimental results and data on life history characteristics suggest that these species compete significantly during periods of drought-induced food scarcity but not at other times. The mechanism of this competition is probably exploitative, with the per capita effect of *S. merriami* on *U. ornatus* greater than vice versa. Temporal variation in the intensity of competitive interaction between these two species is attributable to variation in food resource abundance, and arthropod abundance in this system was shown to be a function of rainfall. Examination of 22 yr of continuous precipitation data suggests that competition between these species may be frequently absent or undetectable in this system.

The results of this study demonstrate that the intensity of interspecific competition can be quite variable in systems such as this and invite caution to the uncritical acceptance of point estimates of the intensity of competitive interaction.

Key words: Chihuahuan Desert; competition; food availability; growth models; individual growth rates; lipid storage; lizards; Reptilia; *Sceloporus*; Texas; *Urosaurus*.

INTRODUCTION

Much of recent ecological theory concerning the structure of natural communities rests on the assumption that the primary organizing factor is interspecific competition (MacArthur and Levins 1964, 1967, MacArthur 1972, Schoener 1975).

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There have been two approaches to the study of interspecific competition in natural populations. The comparative approach asks whether the distribution, resource utilization, and abundance of natural populations in different ecological situations are consistent with competition theory. The practitioners of this approach have amassed five categories of evidence used to infer the importance of interspecific competition in producing the patterns observed in natural communities. The first four involve comparison of the niche ecology of a species in patches of habitat (e.g., islands or mountain tops) shared and patches not shared with

a closely related species. Differences in niche ecology or morphology in the presence of an ecologically similar species are used as evidence of an interspecific competitive effect. (1) Patterns of geographic variation in morphology attributable to ecological character displacement are usually interpreted as evidence of a competitive effect in syntopy (see reviews in Grant 1972a, Dunham et al. 1979). (2) Patterns of niche differentiation in syntopy are usually interpreted as being due to competition arising from the presence in the same environment of an ecologically similar species. Crowell (1962) initiated the quantitative study of niche shifts with his comparison of the avifaunas of Bermuda and eastern North America. Since then many studies have reported differences in morphology, food habits, microhabitat occupancy, and/or foraging tactics when allotopic and syntopic populations are contrasted (e.g., Grant 1968, Terborgh and Faaborg 1973, Cody 1974, Brown 1975, Schoener 1975, 1977, Pianka 1976, and Diamond 1978). (3) Adaptive radiation and convergent evolution are frequently considered the result of niche shifts in colonists which reach habitat islands lacking competing species (e.g., Lack 1947, MacArthur and Wilson 1967). (4) Parapatric distributions in the ranges of two closely related species are usually interpreted as evidence that each species is competitively preventing the other from extending its geographic range (e.g., Cody 1974). The inference is that the range of each is limited by a biotic factor (competition) rather than a physical factor. (5) The final, and perhaps strongest, class of evidence is the direct observation of one species invading the geographic range of a related species with concomitant replacement or niche accommodation as coexistence is established (e.g., Vaurie 1957, Diamond 1978).

The other major approach to the study of interspecific competition in natural populations has been experimental. The practitioners of this approach employ direct density manipulations, through the selective addition or removal of individuals, in attempting to demonstrate the existence of competition between species (see reviews in Grant 1972b, Colwell and Fuentes 1975, Connell 1975, and Smith 1977). Experimental studies have been particularly successful in freshwater aquatic communities (Reynoldson 1964, Hall et al. 1970, Reynoldson and Bellamy 1971, Wilbur 1972, Werner and Hall 1976), marine rocky intertidal communities (Connell 1961a, b, 1974, 1975, Dayton 1971, Menge 1972), and plant communities (Muller 1966). The experimental approach has rarely been applied to the study of terrestrial animal communities, but a few of the more successful studies include those of Inger and Greenberg (1966), Grant (1969, 1970, 1971, 1972b), Jaeger (1970, 1971, 1972), McClure and Price (1975), Schroeder and Rosenzweig (1975), Brown and Davidson (1977), and Smith (1977). These studies have shown the existence of interspecific competition, and

in some cases the mechanism of that competition, in a manner not possible with the comparative approach. The experimental studies of marine communities, in particular, have demonstrated the potentially great influence of predation, environmental variation, and spatial heterogeneity, as well as competition, on community structure.

The advantages of the comparative approach have been discussed by Cody (1974) and Schoener (1974) and include investigation of systems not amenable to experimental manipulation and greater logistic simplicity than normally required by experimental studies. However, I believe the comparative approach to the study of competition as currently practiced has several serious flaws. The practitioners of this approach have widely invoked interspecific competition to account for such diverse phenomena as patterns of ecological character displacement and character release, parapatric distributions, patterns of resource allocation and microhabitat occupancy, degree of niche overlap among syntopic closely related species, interspecific territoriality and aggression, and differences in life histories. A problem arises because these same phenomena constitute the evidence for the widespread importance of interspecific competition in natural communities. The comparative approach standing alone is circular. Further, the observations used to infer an interspecific competitive effect are frequently consistent with alternative explanations not involving interspecific competitive interaction (Miller 1967, Reynoldson and Bellamy 1971, Grant 1972b). Thus, whether these patterns can be used to test the predictions of competition theory is questionable. The comparative method, though useful in formulating hypotheses, is not as powerful as the experimental approach in testing them (Stearns 1977). In this case, the comparative method offers no direct implication of competition as a causative factor in producing the patterns in natural populations interpreted as evidence for competition.

Frequently experimental studies of competition fail to reveal much about the mechanism of interaction where a competitive effect can be demonstrated (Schoener 1974). Experimental studies of competition between natural populations are normally designed to demonstrate the existence of competitive interaction. Once competition is shown to be a contemporary process in a particular system, other experiments (e.g., resource supplementation) or comparative studies can be used to elucidate the mechanism of interaction.

Almost all of the previous studies of competition in lizard communities have been comparative. Studies of the effects of the number of syntopic, potentially competing species on resource allocation, microhabitat occupancy, food habits, foraging biology, niche overlap, and niche width have been carried out by Milstead (1961), Schoener (1968, 1969, 1970a, b, 1974, 1975,

1977), Schoener and Gorman (1968), Pianka (1969, 1973, 1975, 1976), Lister (1976a, b), and Huey and Pianka (1977). The effects of syntopic potentially competing species on patterns of body size in insular lizard populations have been studied by Soulé (1966), Schoener (1969, 1970a, b, 1974), Clover (1975), and Lister (1976a). All of these investigators inferred a causal relationship between the intensity of interspecific competition, measured as the number of syntopic, potentially competing species, and average adult body size (for a contrasting analysis see Dunham et al. 1978). Patterns of character displacement in fossorial skink (*Typhlosaurus*) populations in the Kalahari Desert have been intensively studied by Huey and Pianka (1974), Huey et al. (1974), and Pianka et al. (1978), and attributed to competition.

Following the pioneering efforts of Blair (1960) and Tinkle (1967), numerous workers have documented variation in life histories, population dynamics, and demography both between lizard species (Tinkle et al. 1970, Turner et al. 1970, Vinegar 1972, Ballinger 1973, Smith 1977, and others) and among populations of the same species (Tinkle 1967, Tinkle and Ballinger 1972, Parker and Pianka 1975, Van Devender 1975, Ballinger 1977, and others). Several workers have shown significant variation in individual growth rates and/or life histories related to proximal variation in food resource availability (Martin 1973, 1977, Ballinger 1977, Dunham 1978a, b, Schoener and Schoener 1978). The work of several investigators suggests that different populations of a species may differ greatly in the degree to which they are subject to predation or in the extent to which they are affected by temporal variation in resources (Pianka 1970, Tinkle and Ballinger 1972, Andrews and Rand 1974, Parker and Pianka 1975, Ballinger 1979, and others). These data 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. The comparative studies discussed above suggest that competition may be important in structuring lizard communities, but the evidence is indirect and alternative explanations involving specialization on abundant resources in populations limited to densities well below carrying capacity by predation are available (Schoener 1977). Therefore, direct experimental demonstration of competitive interaction between the species in several types of lizard communities seems necessary to test the hypothesis that competition is a contemporary phenomenon and, therefore, a likely causative factor in producing the patterns of resource allocation, habitat segregation, etc. revealed by the numerous comparative studies of lizard communities.

This study is an attempt to determine experimentally the significance of interspecific competition in a

simple guild consisting of two abundant species of iguanid lizards, the canyon lizard, *Sceloporus merriami* Stejneger, and the tree lizard, *Urosaurus ornatus* Baird and Girard, at a location of ecological microsympatry in southwestern Texas.

This species pair was chosen for an experimental study of interspecific competition because Milstead (1961, 1970) concluded on the basis of similarity in habitat, diet, and behavior that they were probably strong competitors. Further they coexist at relatively high densities, are territorial, and have small home ranges, are easily captured and individually marked, and if study sites are suitably chosen, population densities can be manipulated by selective removal.

METHODS

The study system and lizard community

The study area was located at an elevation of ≈ 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 *Bouteloua brevicata*, *Bouteloua eriopoda*, *Aristida* spp., *Parthenium incanum*, *Diospyros texana*, *Agave lechuguilla*, *Fouquieria splendens*, *Opuntia engelmannii*, *Dasyllirion leiophyllum*, *Yucca torreyi*, *Mimosa biuncifera*, *Viguiera stenoloba*, *Larrea tridentata*, *Prosopis glandulosa*, and *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 consists of at least 12 species: *Eumeces obsoletus*, *Cnemidophorus scalaris*, *Cnemidophorus tigris*, *Coleonyx brevis*, *Cophosaurus texanus*, *Crotaphytus collaris*, *Phrynosoma cornutum*, *Sceloporus magister*, *Sceloporus merriami*, *Sceloporus undulatus*, *Urosaurus ornatus*, and *Uta stansburiana*. The study area and lizard fauna are described in greater detail elsewhere (Dunham 1978b and *in press*).

The iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus* coexist in microsympatry in areas of suitable habitat over much of the Big Bend region of southwestern Texas and parts of the adjacent Mexican states of Coahuila and Chihuahua (Milstead 1961, 1970, Olson 1973, Dunham, *in press*). In the area of syntopy both species are small, saxicolous, diurnal insectivores and in the Grapevine Hills they are the only lizard species in the saxicolous, diurnal insectivore guild (*sensu* Root 1967). Prior to this study the biology of the canyon lizard had received little attention. The tree lizard has been more intensively studied. A number of workers have discussed the reproductive biology of *U. ornatus* including Asplund and Lowe (1964), Martin (1973, 1977), Michel (1976), van Loben Sels (1976), Ballinger (1977), and Smith (1977). Ballinger

TABLE 1. Protocol of the density manipulation experiment showing the area (ha) of each plot and the assignment of the experimental treatments.

Plot	Area (ha)	Experimental treatment
I	0.53	Control
II	0.76	<i>U. ornatus</i> removed; <i>S. merriami</i> unaltered
III	0.66	<i>S. merriami</i> removed; <i>U. ornatus</i> unaltered
IV	0.83	Control
V	1.02	<i>U. ornatus</i> removed; <i>S. merriami</i> unaltered
VI	0.94	<i>S. merriami</i> removed; <i>U. ornatus</i> unaltered

(1976, 1977) and Smith (1977) 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. Tree lizard hibernacula have been described by Worthington and Sabbath (1966) and Vitt (1974). Data on behavior were provided by Carpenter and Grubitz (1960, 1961) and Purdue and Carpenter (1972). Milstead (1970) compared the territorial and reproductive behavior of syntopic *Sceloporus merriami* and *Urosaurus ornatus*. A detailed analysis of the population biology and demography of the populations of *S. merriami* and *U. ornatus* discussed in this paper is presented elsewhere (Dunham 1978b and *in press*).

Potential predators on *S. merriami* and *U. ornatus* in the Grapevine Hills are common and include snakes (*Masticophis lateralis*, *Masticophis flagellum*, *Salvadora grahamiae*, *Crotalus lepidus*, and *Crotalus molossus*), other lizards (*Crotaphytus collaris* and *Eumeces obsoletus*), and birds (*Geococcyx californianus*, *Lanius ludovicianus*, and *Campylorhynchus brunneicapillus*). Of these, only *M. taeniatus*, *S. grahamiae*, *C. molossus*, *C. lepidus*, *E. obsoletus*, and *C. brunneicapillus* were common and probably represent the important predators on the lizard populations studied here. The whiptail lizards (*Cnemidophorus tigris* and *C. scalaris*) were common and probably are important predators on the eggs of *S. merriami* and *U. ornatus*.

During this study daily precipitation data were available from a United States weather station located at Panther Junction, Big Bend National Park at an elevation of 1140 m, 9.3 km southsoutheast of the study area. The weather data for the study area were summarized by Dunham (1978b and *in press*).

The experimental populations

Six comparable study sites were chosen in May 1974 within the area described above and the density manipulation experiment shown in Table 1 was established. These sites were similar in size (Table 1) and

were chosen because they were inhabited by dense populations of *S. merriami* and *U. ornatus* and because each was separated from other such sites by habitat unsuitable for these lizards. The experimental treatments were assigned to the sites randomly, and these treatments were maintained throughout the study. My assistants and I attempted to remove all *S. merriami* from plots designated III and VI, and all *U. ornatus* from plots designated II and V. Densities of the two species were not altered on the control plots (I and IV). At each census of the population remaining on each experimental plot, any individuals of the other species encountered were captured and removed. The Zippen (Zippen 1956, 1958) removal technique of population estimation was used to estimate the initial densities on each experimental plot.

Demography

Populations of *S. merriami* and *U. ornatus* inhabiting the six study plots were censused, at least monthly, from May through September of 1975, 1976, and 1977. In 1974, these plots were censused from May to August. The control plots were censused 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 by noosing. The margins of the study areas as well as the habitat between study areas were intensively searched periodically in an attempt to estimate the frequency of emigration from the study populations. Each new lizard was sexed, given a unique identifying number and 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 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 mentioned data recorded. I took all measurements to minimize error due to differences among observers. Lizards were released 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 (Chapman 1951, Seber 1973). Estimates for early June were used to compare densities on each plot for each year of the study because these are the sampling dates closest to the onset of oviposition.

Bias in recapture estimates of population density 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 varies

as a function of its capture history (Seber 1973). 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 despite 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 was 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 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. Lizards marked shortly after hatching were easily distinguished from older animals by their small size, and frequently by the presence of a yolk scar. These animals could be aged with certainty at each recapture. Most animals were initially 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 (SVL) were polymodal at that time, and the SVL of lizards of known age indicated that, in each case the smaller individuals were in their 1st yr after hatching (the yearling age class) and that the larger animals represented a mixture of older age classes. Some individuals, particularly of *U. ornatus*, were intermediate in size at first capture and could not be aged with certainty. These animals were assigned to the most likely age class given their SVL, subsequent growth history, and the survivorship characteristics of the population to which they belonged. Details of the determination of age structure and demography of these populations are presented elsewhere (Dunham 1978b and *in press*).

Age-specific fecundity

Samples for reproductive data were taken at least monthly from May through September of 1975, 1976, and 1977 and every 2 wk during May to August of 1974 from similar habitat within 2 km of the study plots. In 1976 and 1977 these animals were frozen for later autopsy (see section on storage lipids). Autopsied animals were weighed to the nearest 0.1 g and the SVL measured to the nearest 0.5 mm. Reproductive data were taken at the time of autopsy. Clutch size (number of eggs per clutch) was determined by direct count of oviductal eggs, corpora lutea, or yolked follicles ≥ 4 mm diameter. This size was chosen because follicular atresia was not observed in either species after this size had been attained. Linear regression models of the relationship of clutch size to SVL were construct-

ed for each species. Different models were estimated from the data from 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 plot 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. Reproductive data were also obtained from marked individuals captured on the study plots. Females were palpated for eggs and the reproductive condition was noted at each capture. Frequently females which had recently oviposited could be recognized because they had mud caked on their feet and chin and had lost mass approximately equal to the wet mass of a clutch (0.5–1.0 g) and/or they had changed from a gravid to a nongravid 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.

Storage lipids

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 (corpora adiposa) and liver of each animal were removed and weighed to the nearest 0.1 mg. The stomach and gut contents were removed and the fat bodies, liver, and remaining carcass were dried to constant mass on a freeze-drying apparatus. The carcass was then homogenized by grinding in a Wiley Mill and the lipids in the liver, fat bodies, and a sample of a homogenized carcass were extracted in excess chloroform. The solvent and dissolved lipids were separated in a rotary evaporator and the dry mass of lipid in each compartment determined. Only data from animals in the prehibernation (=brumation) samples (late September–early October) samples are presented here. The total prehibernation lipid storage of an animal was taken to be the sum of the dry masses of chloroform extractable lipid in the fat bodies, liver, and carcass. In early October of 1977, I collected 10–20 males and females of each species from the experimental populations and determined their total prehibernation lipid. This was the only destructive sampling of the populations of marked individuals during this study. Linear regression models relating total prehibernation lipids and wet body mass to SVL were computed using logarithmically transformed variables. The analysis of covariance (ANCOVA) was used to compare these models to analogous ones derived for the control populations.

Survival

For animals 1 yr old or older, annual survivorship was estimated as the ratio of the number in a cohort

of marked animals known to be alive in early June of one year to the number of marked animals in that cohort known to be alive in early June of the previous year. Survival from age 0 to age 1 was estimated as the ratio of the small-sample Lincoln-Peterson estimate (Seber 1973) of the number of yearlings alive on a particular plot in June of a given year to the estimated number of eggs produced by the sexually mature females residing on that plot when clutches were produced the previous year. Survival from hatching to June of the following year was estimated as the ratio of the number of marked hatchlings known to have survived 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

Data from the recapture of marked individuals were used to estimate the free parameters, asymptotic body size (A_1), and the characteristic growth rate (r), of the logistic-by-mass growth model using a nonlinear least squares regression procedure. Details of this type of growth analysis were presented by Dunham (1978a, b) and Schoener and Schoener (1978). Elsewhere, I showed that the logistic-by-mass model provided a better fit (lower residual error mean square) to the recapture data for these two species than did either the Von Bertalanffy or the logistic-by-length model (Dunham 1978a, b). Only recapture intervals longer than 20 d were used in the analysis to minimize the effects of measurement error. SVL was used as the measure of body size. The other possible measure (mass) varies as a function of reproductive condition (especially in females) and recent nutritional history to a much greater extent than does SVL. The differential equations for the logistic-by-mass model employed here describes the change in SVL when mass is changing logistically allowing the model to be fit to data which use SVL as the measure of size. Separate models were fit to the recapture data from *S. merriami* and *U. ornatus* from each study plot. In the absence of significant differences between plots, models were fit to the combined data from each experimental treatment. Models were estimated from the data for each year of the study.

Use of the nonlinear least squares procedure allowed 95% "support plane" confidence intervals to be constructed around the parameter estimates of each growth model because asymptotic standard deviations are computed for each parameter estimated (Marquardt 1964, Dunham 1978a, b, Schoener and Schoener 1978). The support plane confidence interval is the maximum symmetrical confidence interval about a given parameter estimate, regardless of the value of the other parameter in the model. In contrasting different growth models, I considered parameter esti-

mates to be significantly different if the 95% support plane confidence intervals did not overlap. This is an extremely conservative test.

Food availability

As detailed elsewhere (Dunham 1978a, b and *in press*), I used two methods to estimate the abundance of potential prey for *S. merriami* and *U. ornatus*. In 1975, 1976, and 1977 masking tape squares (58.06 cm²) coated with the insect trapping adhesive Tanglefoot™ were affixed to rock surfaces where these lizards normally fed. These traps were used from May to October to estimate arthropod abundance on the control plots (I and IV). On each sampling date, at least 12 traps were used on each area. The exact time each trap was set was recorded. At each reading, the time and number of arthropods trapped were recorded. These data were converted to capture rates (arthropods · trap⁻¹ · h⁻¹) and the null hypothesis of no significant difference in the capture rates of these traps on comparable sampling dates in 1975, 1976, and 1977 was tested using Mann-Whitney U tests. Similar methods have been used by Simon (1975) and Ballinger (1977).

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 arthropod abundance on control plots. During sampling periods, open rock surfaces where *S. merriami* and *U. ornatus* normally foraged were sampled for periods of ≈2 min. On each sampling date, two samples were taken on each control site between 0930 and 1145, the duration of each sample was determined with a stopwatch, and the total number of arthropods captured counted. These data were converted to a capture rate (arthropods/min).

Individual foraging success

I employed three measures of foraging success. The first estimate was the wet mass of the stomach contents of adult male *S. merriami* and *U. ornatus* taken for reproductive data. Data from females were not used because females with large ovarian or oviductal eggs eat very little compared to nongravid females or males, and I timed the collection of reproductive samples to maximize the proportion of such females in the samples. As a result, sample sizes of nongravid females were often too low for comparison and there was no way to control the confounding effect of having both gravid and nongravid females in the samples. Only data from animals taken in 1976 and 1977 are presented here.

The second method of estimating individual foraging success consisted of direct observation of foraging males of both species. My assistants and I observed individually marked males on the control plots in 1976. These observations were carried out between 0800 and

1100 Central Daylight Time, 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 was counted. These data were converted into a feeding rate. In order to have an adequate sample, I lumped these data into samples from three 2-wk intervals (late June, early August, and late August). Simultaneously with the first two samples, I observed foraging males of both species on the experimental areas and estimated their foraging success in the same manner.

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

Demonstration of competitive effects

The criteria necessary to demonstrate interspecific competition directly have been discussed by a number of authors (e.g., Reynoldson and Bellamy 1971, Wilbur 1972, Colwell and Fuentes 1975, Emlen 1975, and Smith 1977). These criteria include changes in population size, measured either as numbers or biomass, population persistence or extinction, or rate of increase. Like Pontin (1963), Wilbur (1972), and Smith (1977), I define competition operationally by its measurable experimental effects. If a decrease in the density of species A causes, all other things being equal, an increase in species B, then a competitive effect of species A on species B has been demonstrated. This approach allows the definition of competition and its demonstration to be independent of consideration of the mechanisms of competition. This definition, while conceptually simple, is plagued with epistemological difficulty arising from the phrase "all other things being equal." Experiments in which all noncompetitive factors (e.g., predation) which potentially affect population density or biomass are kept constant across experimental treatments are logistically difficult to establish and maintain. Further, the populations studied here are small and, as Smith (1977) has pointed out, the sampling distribution of population size is unknown, making statistical tests of changes in population size difficult. Furthermore, the generation times of the two species studied here are long compared to the duration of the experiment and the rapidity of environmental fluctuation in the study system. Therefore, I also accept as evidence of competition changes in life history characteristics, individual growth rate, individual foraging success, body mass, and prehibernation lipid storage which, all other things being equal,

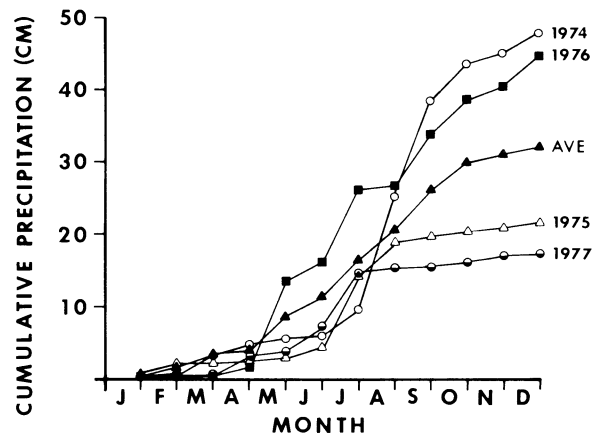


FIG. 1. Comparison of the annual precipitation during the 4 yr of this study. The mean annual precipitation based on 22 yr continuous data is also shown.

would lead to an increase in the density, biomass, or rate of increase of an experimental population when the density of a potential competitor is decreased. The latter category of evidence has the advantage that appropriate statistical tests of the effects of experimental manipulation are more easily devised.

In all statistical procedures used in this analysis, I employed parametric hypothesis tests when the data did not seriously violate the assumptions of those tests. I used analogous nonparametric procedures (Conover 1971) when the assumptions of the appropriate parametric procedures could not be met. In all statistical tests, the null hypothesis was rejected if the attained level of significance was $\leq .05$.

RESULTS

Rainfall and prey abundance

The 4 yr of this study differed greatly in the amount and distribution of precipitation (Fig. 1). The total annual precipitation was 48.01 cm in 1974, 21.41 cm in 1975, 44.65 cm in 1976, and 17.17 cm in 1977. The total active season (April–October) precipitation was 40.89 cm in 1974, 18.14 cm in 1975, 37.21 cm in 1976, and 15.49 cm in 1977. The mean annual precipitation based on 22 yr continuous data is 32.44 ± 4.41 (95% CI) cm; the mean active season precipitation for the same period is 26.82 ± 4.19 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 United States weather station at Panther Junction (1956).

Comparison of sticky trap estimates of arthropod abundance suggests that saxicolous insectivores such as *S. merriami* and *U. ornatus* had significantly more prey available in 1976 than in 1975 or 1977 (Fig. 2). In all cases the mean estimate for a sampling date in 1976

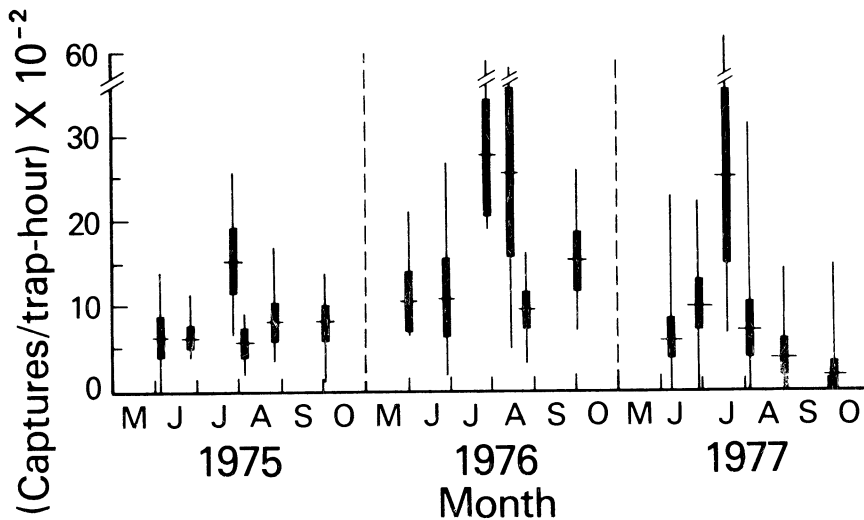


FIG. 2. Tanglefoot™ trap estimates of arthropod abundance on the control plots on comparable sampling dates during 1975–1977. The vertical line is the range, the horizontal line is the mean, and the vertical bar shows the 75% error bounds.

was greater than that for the corresponding sampling date in 1975 and 1977. Mann-Whitney U pairwise comparisons revealed that in all but two cases the differences were statistically significant ($P < .05$). The 1976 estimate for late June was greater than that for the same period but the difference was not significant ($P = .13$). The same was true for the comparison of the late August estimate for 1976 with that for 1975 ($P = .08$). Pairwise Mann-Whitney U comparisons of the mean sticky trap estimates for comparable sampling dates revealed that arthropod abundance was significantly greater in 1976 than in either 1975 ($U = 31$, $.01 \leq P \leq .025$) or 1977 ($U = 33$, $.005 \leq P \leq .01$) but that the estimates for 1975 and 1977 were not significantly different ($U = 15$, $P > .10$).

The two methods of estimating prey abundance were concordant in their estimates; there was a highly significant Spearman rank correlation ($r_s = .83$, $.01 \leq P \leq .003$) between the D-Vac™ and sticky trap estimates for 1976 and 1977. In the 2 yr (1976 and 1977) for which there are data, the highest serial correlation ($r = .646$, $P < .05$) between the D-Vac™ estimate of arthropod abundance and precipitation was with the amount of rainfall in the preceding 2-wk time interval. Neither method provides an unbiased quantitative estimate of 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 and certain taxa (e.g., some orthopterans) tend to flee an approaching D-Vac™ and are thus underrepresented in those samples. However, both methods sample the same array of prey types and sizes as is found in the stomachs of these lizards and thus provide satisfactory indices of the relative abundance of prey available at different times.

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 for at least 3 yr were used to estimate the conditional probability that an individual was captured given that it was known to be at risk. The analysis of catchabilities of these animals is presented elsewhere (Dunham 1978b, *in press*). Of 155 male *S. merriami* known to have survived 3 yr, 149 were captured at least once in the 2nd yr. If these represent a simple random sample of the population alive during the 2nd yr, 96% of the male canyon lizards alive then and previously marked were captured at least once during the active season of the 2nd yr. In contrast, 75 of 84 (89%) of the female canyon lizards known to have survived 3 yr were captured during the 2nd yr. Of 62 male tree lizards known to have survived 3 yr, 61 (98%) were captured during the 2nd yr; only 28 of 34 (82%) female tree lizards were captured during the 2nd yr. The observed differences in catchability of male and female *S. merriami* ($\chi^2 = 4.34$, $P = .037$) and *U. ornatus* ($\chi^2 = 8.35$, $P = .004$) are statistically significant. These differences were obvious in the field. Both species exhibit intraspecific territoriality (Milstead 1970), and during the breeding season (mid-April–early August) males are active in territorial defense and courtship. As a result, they are quite conspicuous and easily captured. 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 adult residents on the control plots (I and IV) in early

TABLE 2. Summary of the number and density of adult *U. ornatus* on the control plots (I and IV) in early June of each year of the study. *AC* is the actual number of animals 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 (animals/ha) based on the number of animals registered and the Lincoln-Peterson estimates, respectively. Density estimates based on the pooled data from both control plots are also presented.

Sex	Year	Plot number	<i>AC</i>	<i>LP</i>	<i>DEN (AC)</i>	<i>DEN (LP)</i>	<i>DEN (AC)</i>	<i>DEN (LP)</i>
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		
Females	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		
Males	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		
Females	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		

June of each year of the study are presented in Tables 2 and 3. For those age classes in which there were too few animals to allow calculation of the Lincoln-Peterson estimate, the total number of animals registered is used as the measure of population size. The densities of adults of each species residing on the control and experimental plots in June of each year are summarized in Fig. 3.

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 proportions of adult lizards which escaped capture when known to be at risk, I do not believe the bias to be serious.

On the other hand, hatchlings of both species were

TABLE 3. Summary of the number and density of *S. merriami* on the control plots (I and IV) in early June of each year of the study. Terminology is as in Table 2.

Sex	Year	Plot number	<i>AC</i>	<i>LP</i>	<i>DEN (AC)</i>	<i>DEN (LP)</i>	<i>DEN (AC)</i>	<i>DEN (LP)</i>
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		
Females	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		
Males	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		
Females	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		

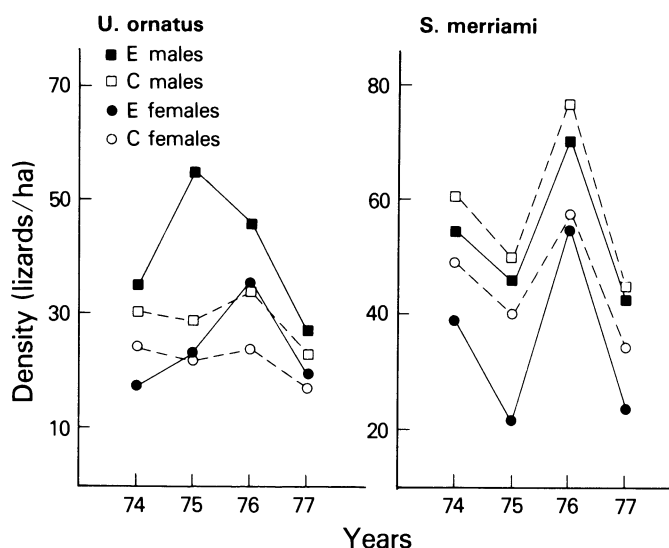


FIG. 3. Summary of the changes in early June densities of posthatchling *S. merriami* and *U. ornatus* on the control (C) and experimental (E) plots during this study.

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, comparisons of small-sample Lincoln-Peterson estimates of the number of hatchlings emerging on each plot in each year should be viewed with caution.

Effects on population density

The densities of adults of both species, as measured by either estimate, fluctuated concordantly on the control areas from 1974 through 1977 (Tables 2 and 3, Fig. 3). The density estimates declined in the years characterized by low rainfall (1975, 1977) and increased in years characterized by higher rainfall (1974, 1976). The variation in density of *S. merriami* was greater than

that of *U. ornatus* on all study plots. There was an average of 116 posthatchling *S. merriami*/ha and 53 posthatchling *U. ornatus*/ha in early June 1974. Zippen's (1956) maximum likelihood estimates of population size (Table 4) indicated that the initial densities of the removed species on the experimental plots were not systematically different from those of the same species on the control plots.

The effects of the removal of *S. merriami* on the densities of *U. ornatus* remaining on the experimental plots were dramatic and both sexes responded concordantly (Fig. 3). Densities of adult *U. ornatus* on the control plots declined slightly from early June 1974 (55/ha) to early June 1975 (50/ha). During the same time interval, the density of adult *U. ornatus* on the experimental plots increased from 52/ha to 80/ha, an increase of 35% over the initial density. Male tree lizards increased from an average of 35/ha to 55/ha

TABLE 4. Estimates of population sizes of lizards on removal areas in early June 1974 based on the maximum likelihood method of Zippen (1956, 1958) with constant sampling effort. N is the number of samples, \hat{p} is the proportion of animals captured in each sample, \hat{n} is the estimated population size ($\pm 95\%$ C. I. half widths), and $V(n)^{1/2}$ is the asymptotic standard deviation.

Species	Removal area	N	\hat{p}	\hat{n}	$V(n)^{1/2}$	Estimated density (lizards/ha)
<i>S. merriami</i>	III	3	0.56	100.00 \pm 9.21	4.70	152.37
	VI	3	0.50	115.91 \pm 14.17	7.18	124.10
	II	3	0.55	101.10 \pm 10.59	5.40	133.41
	V	3	0.48	130.59 \pm 21.20	10.82	127.54
<i>U. ornatus</i>	II	3	0.68	48.21 \pm 2.69	1.37	63.61
	V	3	0.70	59.79 \pm 3.66	1.87	64.02
	III	3	0.64	40.00 \pm 4.32	2.21	60.95
	VI	3	0.63	63.16 \pm 5.15	2.63	67.62

TABLE 5. Summary of 1st-yr survival (*S*) comparisons between control and experimental treatments for 1974–1976. *** indicates $P \leq .001$.

Species	Year	Control			Experimental			χ^2
		Number of eggs	Number of year-lings	<i>P</i> (<i>S</i>)	Number of eggs	Number of year-lings	<i>P</i> (<i>S</i>)	
<i>U. ornatus</i>	1974	434.55	38	0.09	311.48	102	0.32	68.67***
	1975	261.07	64	0.25	449.65	94	0.21	1.26 ^{NS}
	1976	416.91	38	0.09	791.20	34	0.04	11.29***
<i>S. merriami</i>	1974	438.46	63	0.14	371.30	43	0.12	1.38 ^{NS}
	1975	361.10	133	0.37	292.81	154	0.53	16.22***
	1976	525.95	57	0.09	593.59	56	0.09	0.61 ^{NS}

(36%), females from an average estimated density of 17/ha to 25/ha (31%). The proportional change was not significantly different between the sexes ($\chi^2 = 0.14$, $P = .35$). This test is approximate because density estimates were rounded to the nearest integer. From early June 1975 to early June 1976, the density of post-hatchling tree lizards on the control areas increased from 50/ha to 60/ha (16%). On the experimental plots the change in density over the same time period differed between the two sexes (Fig. 3). Posthatchling males declined in average density from 55/ha to 45/ha (18%); posthatchling females, on the other hand, increased from 25/ha to 38/ha (35%). Both experimental and control populations declined sharply in the interval from June 1976 to June 1977. Control populations declined from an estimated adult density of 60/ha to 40/ha (33%), while experimental population densities declined from an average of 83/ha to 44/ha (47%). On both control and experimental plots, the response of the two sexes was concordant; the proportional decline in average estimated density was greater on the experimental plots, but the difference was not significant ($\chi^2 = 2.68$, $P = .102$). The removal of *S. merriami* affected the density of *U. ornatus* in the manner necessary to constitute direct evidence of a competi-

tive effect of *S. merriami* on *U. ornatus*. However, the tenuous nature of the density estimates, the within-treatment variation in density response, and the lack of suitable statistical procedures for analyzing these results invite caution to their acceptance as direct evidence of a competitive effect. Approximate χ^2 tests of whether the control and experimental treatments differed in the proportion of the total density of *U. ornatus* revealed highly significant differences in 1975 ($\chi^2 = 13.85$, $P \leq .0002$) and 1976 ($\chi^2 = 7.40$, $P \leq .007$), with the experimental plots having higher densities in both years. For this test the initial densities were standardized to a common initial density to account for differences in initial density on control and experimental plots. In 1974, before the removal of *S. merriami*, *U. ornatus* was less dense on the control plots but the difference was not significant ($\chi^2 = 0.17$, $P > .5$). Experimental plot *U. ornatus* were more dense in 1977 but the difference was not statistically significant ($\chi^2 = 0.38$, $P > .5$).

There was no evidence that the removal of *U. ornatus* had any significant effect on the density of either of the experimental populations of *S. merriami* for either sex in any year of the study (Fig. 3).

TABLE 6. Comparison of minimal adult survivorship estimates for control and experimental populations. Data on male and female *U. ornatus* are pooled. * indicates $.01 < P < .05$; ^{NS} indicates $P > .05$. *C* indicates data from control plots, *E* indicates data from experimental plots. *m* is the number of animals initially marked, *s* is the number recaptured the following year.

Year		<i>U. ornatus</i>			<i>S. merriami</i> males			<i>S. merriami</i> females		
		<i>C</i>	<i>E</i>	χ^2	<i>C</i>	<i>E</i>	χ^2	<i>C</i>	<i>E</i>	χ^2
1974	<i>m</i>	76	83		80	90		63	65	
	<i>s</i>	31	20	5.07*	45	57	0.89 ^{NS}	22	20	0.25 ^{NS}
	<i>P</i> (<i>S</i>)	0.41	0.28		0.56	0.63		0.33	0.31	
1975	<i>m</i>	68	126		66	68		96	44	
	<i>s</i>	20	38	0.01 ^{NS}	27	42	5.83*	20	17	4.92*
	<i>P</i> (<i>S</i>)	0.29	0.30		0.41	0.62		0.21	0.39	
1976	<i>m</i>	74	130		79	89		69	88	
	<i>s</i>	24	25	4.50*	32	30	0.83 ^{NS}	21	24	0.19 ^{NS}
	<i>P</i> (<i>S</i>)	0.32	0.19		0.41	0.34		0.30	0.27	

TABLE 7. Summary of parameter of estimation for the logistic-by-mass growth models estimated from recaptures of male and female *U. ornatus* from the control and experimental plots. The 95% support plane confidence interval half widths are also presented. \hat{A}_t is the estimated asymptotic snout-vent length, \hat{r} is the estimated characteristic growth parameter, $SSqR/n$ is the residual mean square, and n is sample size.

Treatment	n	$SSqR/n$	\hat{A}_t (mm)	\hat{r}
Males:				
Control				
1974, 1976	158	0.8894	51.07 \pm 0.41	0.0185 \pm 0.0034
1975, 1977	180	0.8435	51.05 \pm 0.55	0.0095 \pm 0.0033
Experimental				
1974, 1976	104	0.9143	51.16 \pm 0.60	0.0194 \pm 0.0042
1975, 1977	98	0.8963	51.02 \pm 0.77	0.0176 \pm 0.0044
Females:				
Control				
1974, 1976	110	1.2341	50.69 \pm 0.78	0.0134 \pm 0.0028
1975, 1977	106	1.3304	50.87 \pm 0.94	0.0062 \pm 0.0011
Experimental				
1974, 1976	86	1.4547	51.05 \pm 1.01	0.0140 \pm 0.0019
1975, 1977	78	1.3910	50.43 \pm 0.88	0.0126 \pm 0.0024

Survivorship

The removal of *S. merriami* had significant effects on the age-specific survival of *U. ornatus* inhabiting the experimental plots. Results of the analysis of differences in 1st-yr survival between control and experimental plots are presented in Table 5; results of the analysis of differences in minimum adult survival are presented in Table 6. First-year survival of tree lizards was significantly higher on the experimental plots for animals born in 1974 ($\chi^2 = 68.67$, $P < .0001$) and lower for animals born in 1976 ($\chi^2 = 11.29$, $P < .001$) than for tree lizards born on the control plots in those years. There was no significant difference in the 1st-yr survival of control and experimental plot *U. ornatus* born in 1975 ($\chi^2 = 1.26$, $P > .1$). The minimal annual survival of adult tree lizards inhabiting the experimental plots was significantly lower than for those inhabiting the control plots in both 1974 ($\chi^2 = 5.07$, $.01 \leq P \leq .05$) and 1976 ($\chi^2 = 4.50$, $.01 \leq P \leq .05$). There was no significant treatment effect on minimal annual adult survival of *U. ornatus* in 1975.

Populations of *S. merriami* also exhibited altered survival attributable to the experimental treatment (Tables 5 and 6). First-year survival was significantly higher ($\chi^2 = 16.22$, $P \leq .001$) for canyon lizards born on the experimental plots (0.53) than for those born on the control plots (0.37) in 1975. There was no significant treatment effect on 1st-yr survival of *S. merriami* in any other year. Both male and female *S. merriami* residing on the experimental plots exhibited significantly higher adult survival from June 1975 to June 1976 than did animals residing on the control plots (Table 6). There was no significant treatment effect on the minimal adult survival of *S. merriami* in any other year of the study.

Individual growth

The logistic-by-mass growth models estimated from the recapture data for control and experimental populations of *U. ornatus* are presented in Table 7. Separate models were estimated for the wet (1974, 1976) and dry (1975, 1977) years of the study. The 95% support plane confidence intervals about the point estimates (\hat{A}_t) of asymptotic body size overlap in all pairwise comparisons, indicating that asymptotic body size did not vary between sexes in any year or between years in either experimental or control populations. There were no significant differences in the point estimate of the characteristic growth parameter (\hat{r}) between the sexes on either the control or experimental plots in any year of the study. Thus, this analysis provides no evidence of significant sexual dimorphism in body size (SVL) in these populations of *U. ornatus*. However, there were significant differences in the estimates of the characteristic growth parameter (\hat{r}) between the control and experimental populations of *U. ornatus* in the dry years (1975, 1977) of this study. Estimates of the characteristic growth parameter were significantly higher for models estimated from the recapture data from animals residing on the experimental plots than were those for models estimated from the data from control populations (Table 7). There was no evidence of an analogous treatment effect on the estimate of r in the models constructed for the wet (1974, 1976) years of this study. The control populations of *U. ornatus* exhibited lower individual growth rates 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 on a given plot in any year.

The results of the analysis of male and female *S.*

TABLE 8. Summary of estimated parameters of the logistic-by-mass models of individual growth of *S. merriami* 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 7.

Year	<i>n</i>	<i>SSqR/n</i>	\hat{A}_l (mm)	\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

merriami are summarized in Table 8 and by Dunham (1978a). There is significant sexual dimorphism in body size (SVL), with males reaching a larger asymptotic body size (A_l). The control populations of both sexes had significantly lower individual growth rates, as estimated by \hat{r} , in the dry years (1975, 1977) than in the wet years (1974, 1976) of this study. There were no significant differences between the point estimates of A_l or r in the logistic-by-mass models estimated from the recapture data from the control and experimental populations for any year of the study. Thus, there is no evidence that the removal of *U. ornatus* had any significant effect on individual growth rates of the *S. merriami* residing on the experimental plots.

Individual foraging success

Wet masses of the stomach contents of adult males sacrificed for reproductive data in 1976 and 1977 are summarized in Fig. 4. There was a significant Spearman rank correlation between the mean mass of food in the stomachs of *S. merriami* and that in the stomachs of *U. ornatus* in both 1976 ($r_s = .94$, $.01 \leq P \leq .02$) and 1977 ($r_s = .94$, $P \leq .01$). There was also a significant correlation between the mean mass of food in the stomachs of *S. merriami* ($r_s = .88$, $P \leq .05$) and *U. ornatus* ($r_s = .83$, $P \leq .05$) and the D-VacTM estimate of prey abundance in 1976. There was also a significant correlation between the mean masses of food in the stomachs of these lizards and the D-VacTM estimate of arthropod abundance in 1977 ($r_s = .89$, $P \leq .02$ for *U. ornatus* and $r_s = .94$, $P \leq .01$ for *S. merriami*). The relationship between the D-VacTM estimate of arthropod abundance and the mean mass of food in the stomachs of adult male tree and canyon lizards is summarized in Fig. 5. There was a significant correlation between estimated food abundance and this measure of foraging success in both *U. ornatus* ($r_s = .87$, $P \leq .02$) and *S. merriami* ($r_s = .85$, $P \leq .02$) for all sampling dates.

TABLE 9. Foraging success of adult males as measured by observed feeding rates during late June, early and late August 1976. *n* is the number of animals observed. Numbers in parentheses indicate the 75% error bounds.

Species	Date	<i>n</i>	Mean feeding rate (strikes/h)
<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 (0.83)
	late August	27	21.45 (0.81)

The second method of estimating individual foraging success consisted of direct observation of foraging males of both species on the control plots in late June, early August, and late August of 1976. Pairwise Mann-Whitney U comparisons revealed that the observed feeding rates of both *U. ornatus* ($U = 596.0$, $P \leq .0001$) and *S. merriami* ($U = 1363.0$, $P \leq .0001$) were lower in late June than in early August (Table 9). Foraging success was also significantly lower in late June than in late August in both the tree lizard ($U = 492.0$, $P \leq .0001$) and the canyon lizard ($U = 783.0$, $P \leq .0001$). The differences in observed foraging rate between early and late August were not significant in *U. ornatus* ($U = 309.5$, $P > .1$), although they were significant in *S. merriami* ($U = 412.0$, $P \leq .02$). Thus, the lower prey abundance in late June (Fig. 2) was reflected in reduced foraging success by individuals of both species.

Results of the comparison of observed foraging success of adult male *U. ornatus* on the control and experimental plots are shown in Fig. 6. These data were taken during the last week of June and the first week of August 1976. Observed foraging rates of animals living on the control and experimental plots were compared using Mann-Whitney U tests and the results are presented in Table 10. Only data from actively foraging animals which were observed for a minimum of 10 min were used in the analysis. The mean D-VacTM estimate of arthropod abundance in late June was 2.86 arthropods/min, that for early August was 16.43 arthropods/min. If these estimates are indicative of the

TABLE 10. Results of pairwise Mann-Whitney U tests for differences in observed foraging rates of adult male *U. ornatus* on experimental and control plots in 1976. Data are in Fig. 6.

Contrast	U	df	P
June vs. August: control	557.0	47	.0004
June vs. August: experimental	466.0	44	.00001
Control vs. experimental: June	504.0	50	.00001
Control vs. experimental: August	230.0	41	.362 ns

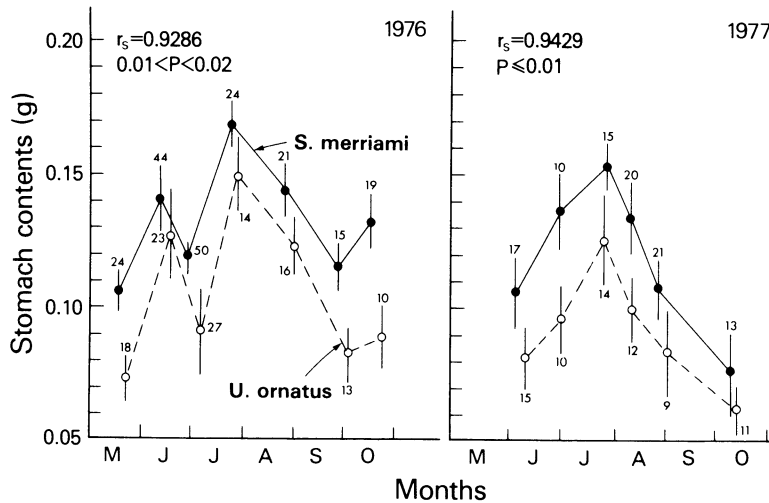


FIG. 4. Mean wet mass of the stomach contents of adult male *U. ornatus* and *S. merriami* on comparable sampling dates in 1976 and 1977. The vertical line shows the 75% error bounds, the dot is the mean, and the numbers are sample sizes. Spearman rank correlations (r_s) compare mean food masses of the two species.

difference in prey availability at these two times, prey were ≈ 5.75 times as available to these lizards in late and early August as in late June. The comparison of foraging rates of animals residing on the control plots showed a highly significant (Table 10) difference in foraging success with the feeding rates of animals observed in August being ≈ 3 times those of animals observed in June. The same pattern was evident when feeding rates of animals residing on the experimental plots were compared (Fig. 6 and Table 10). Observed foraging success of *U. ornatus* on control and experimental plots did not differ significantly when prey were abundant (early August). However, there was a highly significant difference between the feeding rates

of animals on control and experimental plots when prey were scarce (late June). Adult male *U. ornatus* living on the experimental plots exhibited significantly (Table 10) higher feeding rates than did those living on the control plots. Thus, there was a statistically significant treatment effect during times of food resource scarcity and not when prey were abundant.

There was no significant treatment effect on the foraging rates of adult male *S. merriami* in the synchronous comparison. Canyon lizards on both the control and experimental plots had significantly higher feeding rates in early August than in late June.

The final method of estimating individual foraging success involved the quantification of prehibernation storage lipid levels and size-specific body masses in males and females of both species in a wet year (1976) and a dry one (1977). The total body lipid was calculated as the sum of the chloroform extractable lipids in the corpora adiposa, liver, and carcass. These results are presented in Figs. 7 and 8. In males and females of both species, the total prehibernation lipid depends on SVL and the relationship is nonlinear. I used the analysis of covariance (ANCOVA) on the logarithmically transformed variables to compare the size-specific prehibernation lipid levels and body masses of animals collected in different years. The results of this analysis are presented in Tables 11 and 12. In all cases, the size-specific lipid levels and body masses of control animals collected in 1977 were lower than those of control animals collected in 1976 (Table 13). For example, a prehibernation female *S. merriami* which was 50 mm SVL in 1976 would be expected to weigh 3.94 g and to have ≈ 0.28 g (dry mass) of total body lipid. In 1977, the predicted mass of the same female would be ≈ 3.31 g and the predicted total body

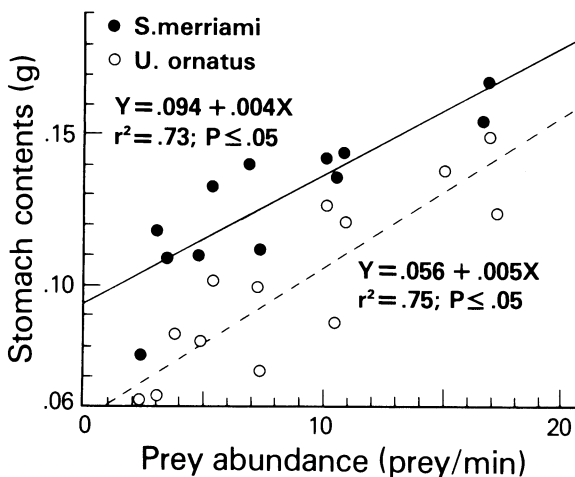


FIG. 5. The relationship between the D-Vac™ estimate of arthropod abundance and the mean mass of stomach contents of adult male *U. ornatus* and *S. merriami*.

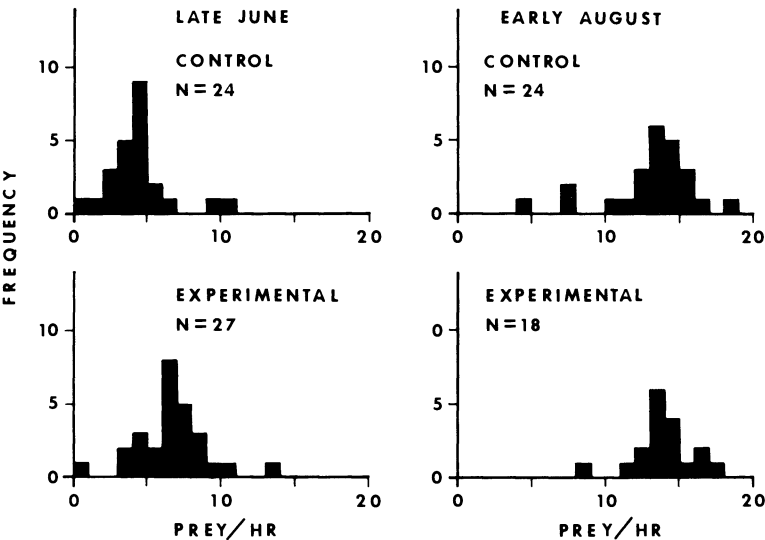


FIG. 6. Comparison of observed feeding rates of adult male *U. ornatus* on control and experimental plots in late June and early August 1976. Statistical comparisons are summarized in Table 10.

lipid would be 0.12 g, corresponding to a body mass difference of 0.63 g (16%) and a difference in total body lipid of 0.16 g (57%). Similar differences were apparent in male *S. merriami* and in both sexes of *U. ornatus* (Table 13).

In addition, covariance analysis revealed that pre-hibernation male *U. ornatus* were significantly heavier in 1976 ($F_{1,20} = 4.35$, $P \leq .05$) than females of the same SVL, although the slopes of the two regression models were different ($F_{1,19} = 10.13$, $P \leq .005$). There was no significant difference in the size-specific body masses of male and female *U. ornatus* in the dry year (1977). Likewise, there was no significant differ-

ence in total prehibernation body lipid between male and female *U. ornatus* of the same SVL in 1976 ($F_{1,20} = 4.28$, $P > .05$) and no difference in the regression models ($F_{2,13} = 2.04$, $P > .1$). However, in 1977 the total prehibernation body lipid was significantly greater in females than in males of equal SVL ($F_{1,17} = 12.63$, $P \leq .002$), and the slopes of the regression lines were not significantly different ($F_{1,16} = 0.02$, $P > .8$).

Covariance analysis of size-specific body masses of prehibernation *S. merriami* revealed that in 1976 males and females did not differ significantly ($F_{1,34} = 19.50$, $P > .1$). The regression models relating the logarithm of body mass to the logarithm of SVL did not

TABLE 11. Summary of the covariance analysis comparing prehibernation body masses and total body lipids of experimental plot *U. ornatus* from 1977 with those of control animals from 1976 and 1977. Regression models are of the form: $\ln Y = a(\ln X) + b$; in all models the covariate is snout-vent length (mm). *** indicates $P \leq .0001$, ** indicates $P \leq .01$, * indicates $P \leq .05$, ^{NS} indicates $P > .05$.

Variable	Sex	Model	a	b	F Statistics		
					Equal regressions	Equal slopes	Equal adjusted means
Prehibernation	Male	1976c	2.497	-8.630	$F_{2,18} = 0.046^{NS}$	$F_{1,18} = 0.020^{NS}$	$F_{1,19} = 0.094^{NS}$
		1977c	2.541	-8.948	$F_{2,15} = 16.107^{***}$	$F_{1,15} = 0.045^{NS}$	$F_{1,16} = 34.209^{***}$
		1977e	2.489	-8.593			
Body mass	Female	1976c	2.007	-6.782	$F_{2,17} = 2.977^{NS}$	$F_{1,17} = 4.208^{NS}$	$F_{1,18} = 1.648^{NS}$
		1977c	1.971	-6.713	$F_{2,16} = 5.033^*$	$F_{1,16} = 2.178^{NS}$	$F_{1,17} = 7.378^*$
		1977e	1.453	-4.590			
Prehibernation	Male	1976c	2.788	-12.649	$F_{2,18} = 12.839^{**}$	$F_{1,18} = 0.254^{NS}$	$F_{1,19} = 23.797^{**}$
		1977c	3.967	-17.927	$F_{2,15} = 43.895^{***}$	$F_{1,15} = 2.213^{NS}$	$F_{1,16} = 99.547^{***}$
		1977e	3.336	-5.032			
Lipids	Female	1976c	2.884	-13.049	$F_{2,17} = 1.667^{NS}$	$F_{1,17} = 2.345^{NS}$	$F_{1,18} = 0.920^{NS}$
		1977c	3.780	-17.162	$F_{2,16} = 25.015^{***}$	$F_{1,16} = 0.518^{NS}$	$F_{1,17} = 52.931^{***}$
		1977c	3.954	-17.280			

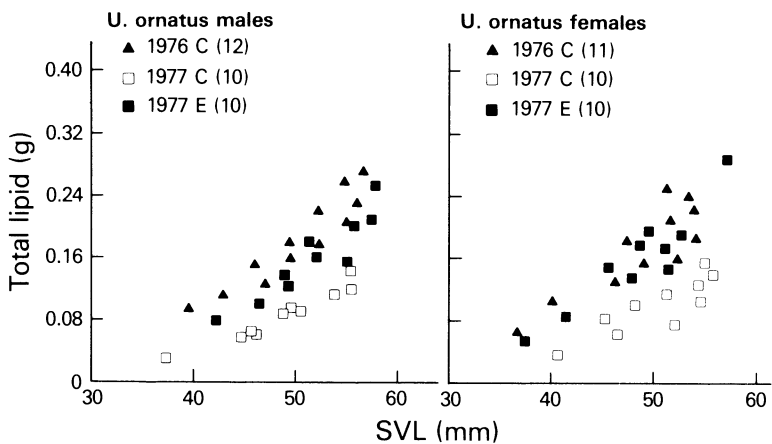


FIG. 7. Data showing a significant (ANCOVA) treatment effect on total prehibernation body lipid in male and female *U. ornatus* in 1977.

differ ($F_{2,33} = 2.24$, $P > .1$). The same result was obtained in the analysis of the data from 1977 ($F_{1,34} = 0.03$, $P > .8$ for adjusted means; $F_{2,33} = 0.55$, $P > .5$ for regressions). The comparison of prehibernation lipid levels in male and female *S. merriami* showed that there were highly significant differences in both 1976 ($F_{1,34} = 42.03$, $P \leq .0001$) and 1977 ($F_{1,34} = 27.82$, $P \leq .0001$). 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 ($F_{1,33} = 4.98$, $P \leq .03$) but not in 1977 ($F_{1,33} = 0.02$, $P > .8$).

The data presented in this section strongly indicate that individual foraging success in these lizards is related to arthropod abundance. The most convincing data are those on prehibernation lipid levels and body masses. Males and females of both species exhibited significantly lower (ANCOVA) size-specific prehibernation total body lipids and body masses in the dry

year (1977). The comparison of sticky trap estimates of arthropod abundance indicated that there was significantly less food available to saxicolous insectivores such as *S. merriami* and *U. ornatus* in 1977. The comparisons of prehibernation size-specific body masses and total body lipid levels strongly suggest that these lizards were less successful in harvesting food resources in 1977 than in 1976.

Effects on prehibernation body mass and lipid storage

The results of the covariance analysis of the prehibernation size-specific body masses and total body lipids of control and experimental *U. ornatus* and *S. merriami* are presented in Tables 11 and 12. These data provide the most convincing evidence of a significant effect of the removal of *S. merriami* on *U. ornatus*. The size-specific body masses and total body lipids of *U. ornatus* collected from the experimental

TABLE 12. Summary of the covariance analysis comparing prehibernation body masses and total body lipids of experimental plot *S. merriami* from 1977 with those of control animals from 1976 and 1977. Terminology is as in Table 11.

Variable	Sex	Models	a	b	F Statistics		
					Equal regressions	Equal slopes	Equal adjusted means
Prehibernation	Male	1976c	2.097	-6.749	$F_{2,30} = 108.78^{***}$	$F_{1,30} = 29.77^{***}$	$F_{1,31} = 97.404^{***}$
		1977c	2.842	-9.927	$F_{2,27} = 0.302^{NS}$	$F_{1,27} = 0.302^{NS}$	$F_{1,28} = 0.310^{NS}$
		1977e	2.949	-10.343			
Body masses	Female	1976c	3.031	-10.501	$F_{2,20} = 56.342^{***}$	$F_{1,20} = 8.657^{**}$	$F_{1,21} = 76.230^{***}$
		1977c	2.612	-9.006	$F_{2,22} = 0.742^{NS}$	$F_{1,22} = 0.696^{NS}$	$F_{1,21} = 0.748^{NS}$
		1977e	2.720	-9.441			
Prehibernation	Male	1976c	4.254	-18.493	$F_{2,30} = 37.194^{***}$	$F_{1,30} = 0.857^{NS}$	$F_{1,31} = 73.870^{***}$
		1977c	4.712	-20.992	$F_{2,27} = 2.916^{NS}$	$F_{1,27} = 1.066^{NS}$	$F_{1,28} = 5.91^{*}$
		1977e	4.894	-21.590			
Lipids	Female	1976c	6.744	-27.585	$F_{2,20} = 19.337^{***}$	$F_{1,20} = 4.528^{*}$	$F_{1,21} = 29.234^{***}$
		1977c	6.194	-26.353	$F_{2,22} = 0.817^{NS}$	$F_{1,22} = 1.392^{NS}$	$F_{1,23} = 0.239^{NS}$
		1977e	4.632	-20.188			

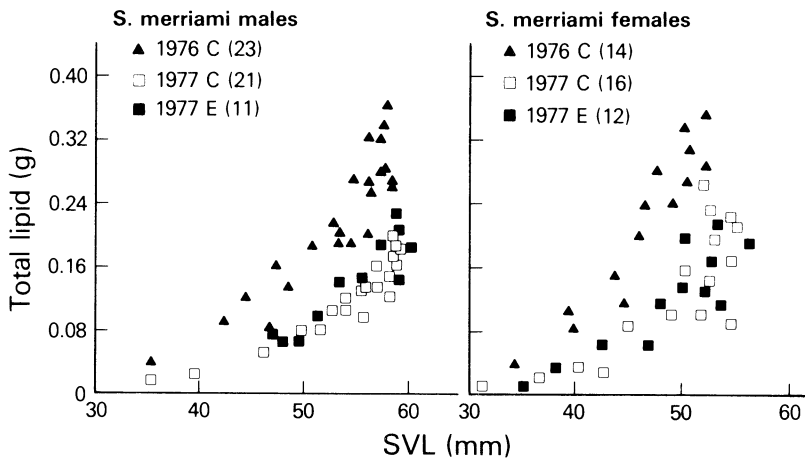


FIG. 8. Data showing the absence of a significant (ANCOVA) treatment effect on total prehibernation body lipid in male and female *S. merriami* in 1977.

plots in October 1977 were compared with those of control animals taken in 1976 and 1977. There was a significant difference (ANCOVA) between the size-specific body masses and total body lipids of experimental plot animals and those of control animals taken in 1977 (Table 11). Tree lizards from the experimental plots had significantly higher size-specific total body lipids and body masses than the control animals captured at the same time. There was no significant difference (ANCOVA) between control plot tree lizards taken in October 1976 and experimental plot animals taken in October 1977, but the control animals taken in 1976 had significantly higher (ANCOVA) size-specific body masses and prehibernation lipid levels than did the control animals taken in 1977 (Table 11). I consider this prima facie evidence of a significant treatment effect and, hence, of a significant competitive effect of *S. merriami* on *U. ornatus* in years of food scarcity. The data on prehibernation lipid levels are shown in Fig. 7.

The corresponding analysis of the data from experimental and control *S. merriami* revealed no evidence

of a significant treatment effect. Both control and experimental plot canyon lizards taken in October 1977 exhibited significantly lower (ANCOVA) size-specific lipid levels (Fig. 8) and body masses than did the control animals taken in October 1976 (Table 12). The size-specific body masses and total body lipids did not differ significantly (ANCOVA) between the experimental treatments in 1977 (Table 12). Thus, these data provide no evidence of a significant treatment effect nor, therefore, of a significant competitive effect of *U. ornatus* on *S. merriami*.

SUMMARY AND DISCUSSION

This study demonstrates that seasonal and annual variation in the amount of precipitation results in predictable variation in the availability of arthropod prey to *S. merriami* and *U. ornatus* which, in turn, results in predictable variation in individual foraging success, individual growth rates, size-specific prehibernation body masses and total body lipid levels. Specifically, in years of reduced rainfall (e.g., 1975 and 1977) and reduced prey availability individuals of both species

TABLE 13. Representative prehibernation body masses and total prehibernation body lipid of female *S. merriami* and *U. ornatus* as a function of snout-vent length (SVL) and year. Values are based on the ANCOVA models in Tables 11 and 12. %D is the percent difference in the response variable when years are contrasted.

Species	SVL	Body mass (g)			Total body lipid (g)		
		1976	1977	%D	1976	1977	%D
<i>S. merriami</i>	50.0	3.88	3.36	13.43	0.300	0.120	60.2
	45.0	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	2.91	2.71	6.87	0.171	0.093	45.5
	45.0	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

exhibited lower growth rates and prehibernation body masses and lipid levels attributable to reduced foraging success during these periods. Results presented elsewhere (Dunham, *in press*) showed that females of both species had lower individual fecundity during dry years.

In addition, this study provides *prima facie* evidence of a significant competitive effect of *S. merriami* on *U. ornatus* during the years (1975, 1977) of reduced prey availability. The density of *U. ornatus* on the experimental plots increased dramatically following the removal of resident *S. merriami* in 1974. This increase was partly due to increased 1st-yr survival of tree lizards born on those areas in 1974. During the same time interval, the populations of *U. ornatus* on the control plots decreased in density and showed no alteration in 1st-yr survival. Individual tree lizards residing on the experimental plots after the removal of *S. merriami* had higher individual foraging success, individual growth rates, and size-specific prehibernation body masses and total body lipids than did *U. ornatus* from the control populations. However, these results were statistically demonstrable only during periods of food scarcity (e.g., during drought years), suggesting that the intensity of the competitive interaction between *S. merriami* and *U. ornatus* is variable and is, perhaps, absent much of the time. The density of *U. ornatus* on the experimental plots after the removal of *S. merriami* was always higher (Fig. 3) than on control plots. Therefore, these results cannot be attributed to changes in the density of *U. ornatus* because, all other things being equal, an increase in the density of conspecific lizards should lead to a reduction in individual foraging success and, hence, individual growth rates and size-specific prehibernation body masses and lipid levels.

The lower annual survivorship exhibited by adult *U. ornatus* following the removal of *S. merriami* is not directly attributable to release from competitive interaction, because the change is opposite in direction to that predicted by competition theory. This result suggests the hypothesis that some predator or set of predators utilize both species as prey and the removal of *S. merriami* resulted in a significant switching of the total predator load to *U. ornatus*. However, this effect was not observed in experimental *S. merriami* populations following the removal of *U. ornatus*, and, therefore, the explanation remains problematic.

There was only one statistically significant treatment effect in experimental populations of *S. merriami* that might be attributed to competitive interaction. Both minimal adult survival and 1st-yr survival were significantly higher in experimental populations of *S. merriami* than in control populations in 1975, the only dry year for which survivorship data are available. These results are consistent with the predictions of competition theory, but in the absence of supporting

evidence in the form of concordant changes in population density, foraging success, prehibernation lipid levels, etc., the case for a significant competitive effect of *U. ornatus* on *S. merriami* is far from overwhelming.

The mechanism of interaction between these two species is not known. The frequency of interspecific agonistic behavior between *S. merriami* and *U. ornatus* is very low (Milstead 1970, A. E. Dunham, *personal observation*), suggesting that, when it occurs, competition between these species is probably exploitative, rather than interference (*sensu* Park 1954). The fact that the life histories and population dynamics of the Grapevine Hills populations of these two species are so similar (Dunham 1978b and *in press*) and that they respond dramatically and concordantly to variation in food availability suggests that both populations are food limited during times of food scarcity (e.g., drought years). That significant effects of the removal of one species are detected only during periods of relative food scarcity suggests that these two species compete for food and that the intensity of that competition is not constant over time. Both intra- and interspecific competition should be severe when resource demand/supply ratios are high resulting in reduced individual foraging success. The resource demand/supply ratio is a result of the interaction of lizard density with food availability. In the present system, therefore, particularly intense competition both within and between species should occur in years (e.g., 1975 and 1977) in which dense lizard populations experience reduction in prey availability induced by drought.

The weak and equivocal response of *S. merriami* to the removal of tree lizard populations requires explanation and there are but two. The first is that there was no competitive effect of *U. ornatus* on *S. merriami* during this study and that the increased age-specific survival exhibited by canyon lizard populations on the experimental plots is due to some other factor. It is possible that mobile predators left the experimental plots to forage in more lucrative areas after the removal of the tree lizard populations. This possibility is suggested by optimal foraging theory (e.g., MacArthur and Pianka 1966) but seems unlikely due to the lack of a concordant response in experimental *U. ornatus* populations following the removal of *S. merriami*. If other noncompetitive explanations exist, they remain obscure. The other possibility is that there was a significant competitive effect of *U. ornatus* on *S. merriami* but that my observational and statistical methods were inadequate to detect it in the range of intensities occurring during this study. Canyon lizards are heavier (ANCOVA, $P < .0001$) for a given SVL than tree lizards (Table 13) and were more abundant on the control areas throughout this study and on the experimental areas prior to removals. Therefore, the biomass of saxicolous iguanid insectivores removed

from the experimental areas was less on those areas from which *U. ornatus* was removed than was the case on areas from which *S. merriami* was removed. The per capita effect of release from interspecific competition was, therefore, likely to be significantly less on canyon lizards than on tree lizards. Significant effects of experimentally induced release from competition from syntopic tree lizards might be readily detectable under conditions of higher resource demand/supply ratio (e.g., more severe drought occurring when lizard populations were especially dense) than occurred during this study. However, the study area received less rainfall in 1977 than in any year since the establishment of a weather station at Panther Junction (1956), and 1975 was as severe. Twelve of the 22 yr for which there are data received less than the mean annual rainfall (32.44 ± 4.41 cm) and six received <28.03 cm ($\bar{x} - 95\%$ C. I.). If the competitive effects of *S. merriami* on *U. ornatus* and vice versa are detectable only in years approaching the severity of 1975 and 1977, competition between these two species may occur infrequently and would probably be detectable by the methods employed in this study even less frequently. However, although 1975 and 1977 were extremely dry years, 1974 and 1976 were extremely wet years and the study area received more rainfall in 1974 than in any year for which data are available. The distribution of precipitation during this study makes estimation of a threshold of year quality below which competitive effects would be detectable by the methods used here impossible. Nonetheless, the data provided by this study argue strongly that the intensity of interspecific competition is quite variable as a function of time in systems such as this and invite caution to the uncritical acceptance of point estimates (e.g., measures of realized niche overlap) of the intensity of competitive interaction when those estimates are based on data collected only at a single point in time or in systems in which the underlying resource dynamics are not measured.

Results like those presented here and those of Wiens (1977) suggest that interspecific competition can be quite variable in intensity and, perhaps, absent much of the time in natural communities. Therefore, long-term experiments combined with comparative studies of patterns of resource utilization seem essential if the variation in the frequency and/or intensity of competition, the mechanisms of competition, or the long-term importance of competition in influencing species coexistence, patterns of resource allocation, and, therefore, community structure are to be adequately assayed. The role of competition in species persistence in the present system is difficult to determine but the results presented here suggest that it may be less important than predicted by current ecological theory. Adequate testing of competition theory in communities of terrestrial vertebrates will require a

long-term approach coupled with a level of resolution not achieved in any study to date.

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