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**Two populations of the tree lizard (*Urosaurus ornatus*) in southern
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The University of Arizona, 1988

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TWO POPULATIONS OF THE TREE LIZARD (UROSAURUS ORNATUS) IN SOUTHERN
ARIZONA

by

Peter Alfred Holm

A Thesis Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE
In the Graduate College
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ABSTRACT

Two populations of the tree lizard (Urosaurus ornatus) were studied in southern Arizona at an urban site--University of Arizona Campus--and a natural desert riparian community at Agua Caliente Wash east of Tucson. The urban site offers greater food and moisture availability, an extended growing season, reduced risk of freezing, and reduced predator diversity with no snakes. In contrast with the desert population, the urban population exhibits greater mean and maximum body size, adult survival, longevity, egg clutch size, and population density. It also exhibits reduced egg to adult survival with some mortality due to nest site competition by adult females. Demographic differences between the two populations do not require evolutionary explanations, having arisen in ecological time.

On an intrapopulation level, males and females differ in body size growth patterns. Male growth is best described by a von Bertalanffy growth model and female growth is best described by a logistic growth model. This sexual dimorphism in growth is correlated with greater relative surface activity and lower survivorship of juvenile males when compared to juvenile females. A comparison of early- and late-hatching offspring suggests that early-hatching (first clutch) offspring exhibit greater body size and survivorship compared to late-hatching (second clutch) offspring.

INTRODUCTION

The tree lizard Urosaurus ornatus is an abundant and conspicuous lizard that appears in more localities in the state of Arizona than any other reptilian species. It can be observed on trees, shrubs, rocks and other elevated substrata extending upslope on a single stream bank from desertscrub into montane conifer forest--from the Lower Sonoran Life-zone to the Canadian Life-zone. Along this same transect several species of syntopic spiny lizards (Sceloporus) will appear and then drop out in distribution, each being restricted to a narrower ecological range as clearly measured in elevation. Moreover, U. ornatus is also present, more often than other species, at localities within the ecological and geographical ranges of other species. Primarily because of small body size, populations of U. ornatus appear to build greater numbers and utilize a wider range of habitat and food resources than those of sympatric larger-bodied taxa.

It is most desirable to have an extensive view of the natural history of a species before specific theoretical questions are profitably explored. Some early and extensive investigations of lizard populations are provided by Blair (1960) on Sceloporus olivaceus, by Zweifel and Lowe (1966) on Xantusia vigilis, and by Tinkle (1967) on Uta stansburiana. Since the late 1960's, these studies and others have provided a basis for constructing theories of life-history evolution in lizards.

Tinkle et al (1970) summarized two general reproductive strategies common to lizard populations. One, thought to be analogous to r-selected, is characterized by small body size, early maturity, multiple clutches per season, and short life expectancy. The other, thought to be more K-selected, emphasizes larger size, delayed maturity, a single clutch, and greater life expectancy. Ballinger (1976), Michel (1976), and Dunham (1980) placed Urosaurus ornatus in the small bodied, early maturing (r-selected) category.

Synthesis of lizard life-history data has revealed that some variation in reproductive effort appears to be explained by morphological adaptations, body size, phylogeny, expected survivorship, and climate (Tinkle 1969, Tinkle et al 1970, Dunham and Miles 1985, Vitt and Congdon 1978, Vitt and Price 1982, Congdon et al 1982, Ballinger 1983, and Stearns 1984). Except for territorial behavior, little is known about density-dependence and carrying capacities in lizard populations, making it difficult to test many predictions of the r- K-selection theory of MacArthur and Wilson (1967).

Fitness is realized differently in males and females. That is, males must survive, defeat rivals, and successfully mate; females must survive and successfully produce eggs. The adaptive trade-off between survival and activities related to reproduction is expected to differ between males and females.

Regardless of proximate causation, variation in life-history traits will contribute to the maximum number of offspring being produced. Increased fecundity and adult survival is expected to result in greater population density and egg to subadult mortality. Comparison

of sexual and interpopulation differences in growth, activity, survival, and reproduction should offer insight into some components of life-history and population regulation.

The purpose of this study was to gather data on age, size, reproduction, and behavior of Urosaurus ornatus for two demographically different populations. The data are used to construct growth trajectories, life tables, and relative surface activity patterns. These results provide a basis for explaining the observed life-history of U. ornatus and some of the differences between sexes and populations. The urban site in this study provides a natural experiment offering recently imposed conditions favorable to increased growth and adult survival; the secondary effects on other demographic parameters are evaluated. An attempt is made to justify or reject an r- K-species classification of U. ornatus and of other lizards.

Urosaurus ornatus is a small, multiple-clutched, semi-arboreal, iguanid lizard. The tree and brush lizards of the genus Urosaurus are among some of the smallest semi-arboreal lizards in North America. Small size and slender form are characteristics of many arboreal and semi-arboreal lizards foraging for insects in the outer fringes of plant canopies and on the stems of small and large plants. Mass and form may be critical to their survival in areas limited to small trees and shrubs and where larger trees and trunks are dominated by other often larger species. The genus Urosaurus is similar in life-form to the more tropical Anolis, however the reproductive cycle of Urosaurus is better adapted to a seasonally variable and temperate climate.

Phylogenetically, the genus Urosaurus shares more recent common ancestry with Sator and Sceloporus, which are also semi-arboreal. It is more distantly related to Petrosaurus and Uta, which are terrestrial and saxicolous. As a whole, the sceloporine group appears to have originated in what is now Mexico, in a region of mixed sclerophyllous and tropical deciduous vegetation.

Three species of Urosaurus occur in the United States, and all of the ten recognized species are found in Mexico. The tree lizard U. ornatus (Fig. 1) occurs from southwestern Wyoming to southern Sinaloa, Mexico, and from just west of the Colorado River in California to central Texas. The densest populations are found in vegetation in Lower and Upper Sonoran riparian woodlands, and in newly formed urban areas. U. ornatus also inhabits rock outcroppings and, in low density, to over 9000 feet (2743 m) on sunlit rock outcrops and dead trees in coniferous forest.

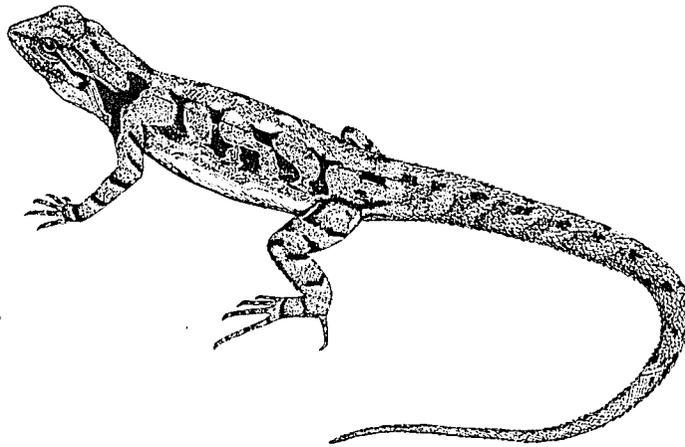


Fig. 1. Urosaurus ornatus, showing adult male.

THE STUDY AREAS

The Tucson (on-campus, urban) and Agua Caliente (off-campus, desert) study areas were selected because of an abundance of tree lizards, field accessibility, and a pronounced difference between the two populations in the body size distributions of individuals. Both sites are in southeastern Arizona in Pima County.

Tucson

The Tucson study area is located on the western side of the University of Arizona campus at an elevation of 739 m. This site is approximately 400 m in length and 40 m in width; excluding pavement, it covers about 1.4 ha. The "anthropology wall" area in Fig. 2 faces southeast and is the best station for sampling at this site. A dense vegetative canopy covers a much greater proportion of the Tucson site than at the Agua Caliente site.

The Tucson site has been entirely landscaped and is well maintained. Grass lawns, cement walks, and limited exposed soil provide the principal habitat floor. Predominant tree and shrub species include the olive (Olea europaea), several palms (mostly Washingtonia filifera), various Eucalyptus, several pines (mostly Pinus halepensis), deodar cedar (Cedrus deodara), some Pyracantha, and others. In addition to the vegetation, there is about 450 m of stone wall much of which lies at the periphery of the study area. Lizard movement is restricted by heavy



Fig. 2. The urban Tucson study site showing the "Anthropology Wall" area southwest of the Anthropology Bldg. on the University of Arizona campus.

motor vehicle traffic to the west. Migration eastward, across campus, is facilitated by nearly continuous landscaping.

Agua Caliente

The Agua Caliente site is located directly east of Soldier Trail Road on the northern floodplain of Agua Caliente Wash at an elevation of 815 m. It covers approximately 350 m of floodplain, and extends from the sand channel to an average of 60 m from the bank; the area is approximately 1.6 ha. Primary productivity of the overall surroundings is primarily concentrated in the nearly linear riparian woodland.

Vegetation in this woodland is characterized by sycamore (Platanus wrighti), Arizona walnut (Juglans major), velvet ash (Fraxinus pennsylvanica velutina), and netleaf hackberry (Celtis reticulata). In addition to these obligate riparian species are mesquite (Prosopis juliflora velutina), desert hackberry (Celtis pallida), catclaw (Acacia greggi), desert-thorn (Lycium andersoni), desert-broom (Baccharis sarothroides), creosotebush (Larrea divaricata), tree cholla (Opuntia versicolor), foothill paloverde (Cercidium microphyllum), and sahuaro (Carnegia gigantea). Mesquite clearly predominates in the study area, but several "islands" of deciduous riparian trees (Fig. 3) form closed canopy habitats with more mesic conditions. These small "islands" are generally separated from the mesquite woodland by up to 10 m of open sand and occasional scrub.

The wash flows intermittently and occasional severe flooding causes substantial damage to the vegetation and alters the structural habitat close to the ground. During my study, several large trees were washed away and others knocked over. The resulting fallen trees and



Fig. 3. The natural riparian community at the Agua Caliente Wash study site.

washed-up brush piles provided some of the most productive areas for sampling and observing lizards on the study site. In contrast to the Tucson site, there are no large rocks that are utilized by tree lizards at Agua Caliente.

Microenvironments at the Study Areas

Xeric conditions are substantially reduced at the Tucson site; the grassy grounds are irrigated regularly. Sunrise and sunset occur several minutes earlier at the Tucson site where the Tucson Mts are to the west. They occur later at Agua Caliente with the Rincon Mts to the east. Some areas within the Tucson site are between large buildings and therefore receive considerably less direct sunshine. Other sites, adjacent to the structures, receive increased nocturnal infrared re-radiation. Some heat loss in the campus study area is also undoubtedly prevented by its richer vegetative canopy. An urban heating effect in Tucson and the pooling of cool air in Agua Caliente Wash results in higher overnight low temperatures at Tucson. Mean monthly minimum and maximum temperatures at the campus site are 11.4 and 28.5 °C. Tucson Magnetic Observatory (TMO) is the closest station to Agua Caliente, reporting mean monthly minima and maxima of 9.9 and 28.5 °C. The average number of days per year with temperatures ≤ 0 °C at Tucson and TMO are 47 and 29 respectively.

The risk of a lizard freezing at the Tucson campus site is considerably lower, and is further reduced by the availability of numerous shelters in stone walls providing thermal buffering (inside minus outside temperature). Simultaneous measurements of temperatures inside and outside of known lizard shelters at the two study areas were

recorded at 0615 - 0645 hrs on April 10, 1986. Mean thermal buffering and outside ambient temperature for rock crevices at Tucson were 6.42 and 10.32 °C respectively. Mean thermal buffering and outside temperature for holes in mesquite wood at Agua Caliente were 3.40 and 5.82 °C respectively.

Predators at the Study Areas

There is a significant and dramatic difference in the diversity of effective predator taxa between the Agua Caliente (off-campus, desert) and Tucson (on-campus, urban) sites. At Agua Caliente, 16 (100%) of the lizard-predator taxa, observed at both sites, occur, compared to 4 (25%), at Tucson (Table 1).

Reptiles.--Nine known Urosaurus-eating reptiles occur in the natural habitat at Agua Caliente; none were observed at the urban Tucson site during the period of study or for many years before. During the period of study, at Agua Caliente 19 observations were made on 7 species of lizard-eating snakes, and 32 observations on 2 species of lizard-eating lizards. The diurnal racer Masticophis flagellum was observed 11 times at Agua Caliente, and on several occasions, while foraging in the canopies of trees where individuals of Urosaurus had been marked.

Birds.--Only two lizard-eating birds, the native mockingbird, and roadrunner (one, seen twice) were observed to work the campus study site during this investigation. The two direct observations of predation by a mockingbird appeared to involve juvenile-sized lizards in the spring. A portion of the study area was aggressively defended by a pair of mockingbirds against intrusion by other birds.

Table 1. Lizard-eating vertebrate animals. Observed species at Urosaurus ornatus study sites in Pima County, Arizona.

Predators	Tucson, central city			Agua Caliente Wash, riparian woodland		
	D	N	D+N ¹	D	N	D+N ¹
Snakes	none					
<u>Masticophis flagellum</u>				X		
<u>Masticophis bilineatus</u>				X		
<u>Salvadora hexalepis</u>				X		
<u>Hypsiglena torquata</u>					X	
<u>Trimorphodon biscutatus</u>					X	
<u>Pituophis melanoleucus</u>						X
<u>Lampropeltis getulus</u>						X
Lizards	none					
<u>Sceloporus clarki</u>				X		
<u>Sceloporus magister</u>				X		
Birds						
<u>Geococcyx californianus</u>	X			X		
<u>Lanius ludovicianus</u>				X		
<u>Mimus polyglottus</u>	X			X		
<u>Falco sparverius</u>				X		
<u>Otus asio</u>					X	
Mammals						
<u>Homo sapiens</u> ²			X			X
<u>Felis domesticus</u>			X			X

1. Diurnal, Nocturnal, Diurnal + Nocturnal.

2. Non-dietary predator.

In a recent study of urban vs. desert populations of birds in the Tucson area, Emlen (1974) recorded a 26-fold increase in numbers and biomass in the urban environment. By the 1970's, as expected, 95% of the in-town bird community consisted of urban-adapted exotics and widespread North American species favoring mesic environments. Native ("desert") species unable to persist in the urban environment have specialized niche requirements in natural communities. Overall diversity of the urban bird community was lower, following a strong filter action on native species in this century.

Mammals.--Some cats and humans exhibit predatorial behavior toward tree lizards. Numerous observations of humans, feral cats, and other domestics suggest that they were not significantly effective predators at either site. An impact of native mammalian taxa is not known; it is assumed to be insignificant or absent.

METHODS

The field work for this investigation was conducted from September 1977 to August 1984. At Tucson, 576 lizards were marked. There were 452 recaptures for a total of 1028 captures. At Agua Caliente, 389 lizards were marked and a total of 477 captures were made. A total of 1504 lizards were measured to the nearest 1.0 mm or 0.1 mm for snout-vent length, total tail length, and tail regeneration. And 1007 lizards were weighed to the nearest 0.1 g or 0.01 g.

Lizards were captured by noose using linen thread. In some instances, especially with hatchlings, lizards were "tricked" onto clothing and then caught by hand. Tails were rarely broken in capture. Individuals were marked, using the method of Zweifel and Lowe (1966), initially by clipping two toes, not on the same foot, and avoiding the specialized elongate fourth toe. As the study progressed, it became necessary to remove three and eventually four toes to provide each animal with unique identification. Lizards with natural toe loss were occasionally given additional toe-clipping to insure later recognition, and placed in an out-of-sequence category. During periods of extended behavioral observation, lizards were marked with nail polish to permit identification without capture.

Specific locations on-site were recorded for each capture. Trees and other structural features were mapped and each station was assigned a number. The reproductive condition, color-pattern, and injury marks were also recorded for each capture. Deep body

temperatures were measured to the nearest 0.1 °C for 55 lizards at Tucson. Environmental temperatures, lizard albedo (light-colored or dark-colored), illumination of perch site (sun or shade), percent cloud cover, wind-movement, and behavior were also recorded at various times. Four 10 X 10 cm sticky traps were placed at each site for one full day in April to sample potential insect prey.

Data reduction and analysis was performed using DEC 10 and Cyber main-frame computers. The more involved graphical and linear regression analysis used SPSS--Statistical Package for the Social Sciences version 8.3.0--May 4, 1982. Nonlinear regression analysis used BMDPAR--Derivative-free Nonlinear Regression version BMD83AR,B. October, 1983. The Z statistic (normal approximation to the binomial) was used to evaluate sex ratios. Contingency was evaluated using the Yates corrected form of χ^2 . Statistical tables used here are those provided in Wynne (1982).

I used the Von Bertalanffy, logistic-by-length, and logistic-by-weight curves to describe growth patterns in Urosaurus ornatus. These models provide parameter estimates of asymptotic body size and characteristic growth rate. The mathematical functions that describe growth, and the methods of fitting them to the data, are provided in Appendix A. Some additional calculations appear in Appendix B. Methods regarding decision making appear in the results and discussion for the specific analyses to which they apply.

RESULTS AND DISCUSSION

PART I. SIZE AND GROWTH

Body size and growth are of great importance to the understanding of life-form (survival), life-history (generally female reproductive success), and sexual selection (generally male reproductive success). Among individuals of both sexes, survival and reproductive success are expected to increase with body size. The mean and variance of body sizes in a population are an indicator of the collective effects of environmental and biological factors influencing growth and survivorship. Differences in body size and growth between individuals, sexes, and populations are explored in this section.

The general literature provides data for many reptilian species on size at birth, at sexual maturity, and the maximum attained. In the American Southwest, iguanid lizards range in adult snout-vent length (SVL) from 40 mm in the genus Uta (Tinkle 1967) to well over 300 mm in herbivorous iguanines such as Ctenosaura and insular gigantic Sauromalus (Case 1983). Several species of insectivorous and semi-arboreal spiny lizards (Sceloporus) reach well over 100 mm in SVL. The tree lizard is a small species. The smallest gravid female measured in this study was 44 mm SVL.

Recapture data permitted resolution of most individuals in both study populations into age classes, such as young-of-the-year, one-year-olds, and two (or more)-year-olds. Lizards marked at an early

age (e.g. SVL < 40 mm) were used to establish guidelines for subsequent age determination. At the Tucson population, 2.9% of the known adult males and 2.6% of the known adult females are smaller than 52 mm and 49 mm SVL respectively. I assumed all males no larger than 51 mm SVL, and females no larger than 48 mm SVL, to be less than one year old. Similarly, for the Agua Caliente population, I assumed all males no larger than 49 mm SVL, and females no larger than 46 mm SVL, to be less than one year old. Some larger individuals, captured only once in the study, could not be aged because of the occurrence of overlapping size distributions among adult age classes.

The Proportionality of Weight and Length

The proportionality of weight and length is useful for comparing populations and subgroupings within a single population. One would expect body weight to increase with the cube of the snout-vent length if juveniles were geometrically similar to adults. Animals with a comparatively greater proportion of weight are either more robust structurally (such as adult males) or possess accumulated food reserves that may be converted into growth, offspring, or energetically expensive activity. Proportionately lighter animals may be structurally "thinner" or low in stored reserves following oviposition, hibernation, or some other period of reduced foraging. This may reflect competitive ability as well as overall effects of climate and food abundance.

Some variation in body weight of animals in the field results from variation in the amount of food in the gut. The mass of stomach contents in specimens prior to fixation account for up to 10% of the

total body mass. Some recaptured males and females exhibit weight loss greater than 10% during summer months.

Log body weight was regressed on log snout-vent length for all males, all females, nonreproductive females, gravid females, and post-partum females. Regression data (Table 2) show a linear relationship of log body weight on log snout-vent length ($r = 0.99$) for both males and all females at the Tucson population. The slopes for males (3.09) and for nonreproductive females (2.94) are significantly different. Adult males differ more from the juvenile form than do adult females. As in many lizard species, males are more robust, have wider heads, and are more muscular, generally.

Smaller females appear to gain relatively more weight for reproduction while larger females appear to lose relatively more weight during oviposition. The slopes (Table 2) are 2.54 for gravid females and 2.70 for post-partum females at Tucson. Larger gravid females and smaller post-partum females do not appear very different in weight/length proportion from nonreproductive females--where the regression lines intersect. The pattern (slope < 3.0) for gravid females is supported by the fact that clutch size varies linearly with SVL, therefore relative clutch mass decreases with increasing SVL (Part II). A bias may result from the observer's ability to recognize gravid and/or post-partum females of different sizes.

The pattern at Agua Caliente is similar when comparing population subgroups. The slopes for males and all females differ significantly between the two populations. Lizards at Tucson not only

Table 2. Regression data reductions for body weight and snout-vent length in Urosaurus ornatus where $\log(\text{BW}) = a + b \log(\text{SVL})$.

	N	r ± SE	a ± SE	b ± SE
Tucson Population				
All males	342	0.99 ± 0.06	-4.64 ± 0.03	3.09 ± 0.02
All females	355	0.99 ± 0.06	-4.50 ± 0.04	2.99 ± 0.02
Non-reproductive females	247	0.99 ± 0.06	-4.43 ± 0.04	2.94 ± 0.02
Gravid females	83	0.77 ± 0.05	-3.68 ± 0.40	2.54 ± 0.23
Post-partum females	20	0.80 ± 0.05	-4.05 ± 0.84	2.70 ± 0.48
Agua Caliente Population				
All males	143	0.99 ± 0.04	-4.42 ± 0.06	2.96 ± 0.04
All females	123	0.98 ± 0.06	-4.16 ± 0.08	2.78 ± 0.05
Gravid females	15	0.73 ± 0.03	-3.22 ± 0.99	2.26 ± 0.58

reach greater SVL but adults are also proportionately heavier for their length.

Variation in Body Size

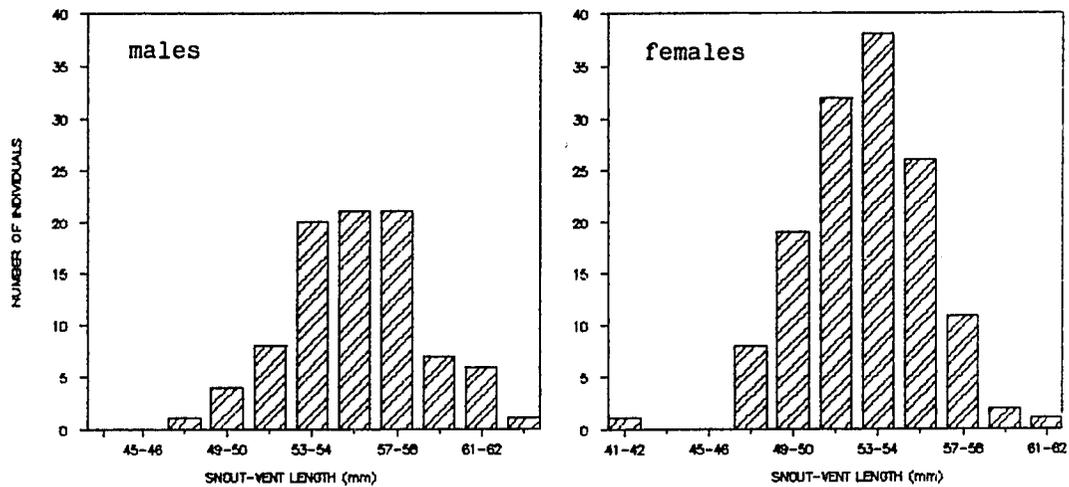
The mean and range of SVL varies between seasons, age groups, broods, sexes, and populations. The frequency distributions of adult SVL in the summer (June 20 - Sept 30, Fig. 4) generally follow a normal distribution, despite the presence of different age classes. Individuals with multiple captures have SVL averaged, so they could be counted only once per year.

Seasonal Patterns

Young-of-the-year are easily distinguished from adults in the late summer and fall distributions illustrated in Fig. 5. One juvenile male at Tucson reached 51 mm SVL in December of its year of hatching. Adult females are under-represented (less surface active) in the spring. Larger adult lizards appear to be under-represented in the fall season. Mean SVL of Tucson males in summer is 55.91 mm compared to 54.56 mm in the fall; the difference is marginally significant ($Z = 1.91$, $P = .06$.) Mean SVL of Tucson females in summer is 53.26 mm compared to 52.01 mm in the fall; the difference is significant ($Z = 2.39$, $P < .05$.) Smaller adults may be attempting to "catch up."

At Tucson, hatchling-sized lizards (SVL < 25 mm) appeared as early as August 4 and as late as November 7. The presence of a few slightly larger juveniles early in August suggests that some may hatch in late July. At Agua Caliente hatchlings appeared from July 25 to October 31. Data from eggs hatched in the laboratory and hatchlings

Tucson



Agua Caliente

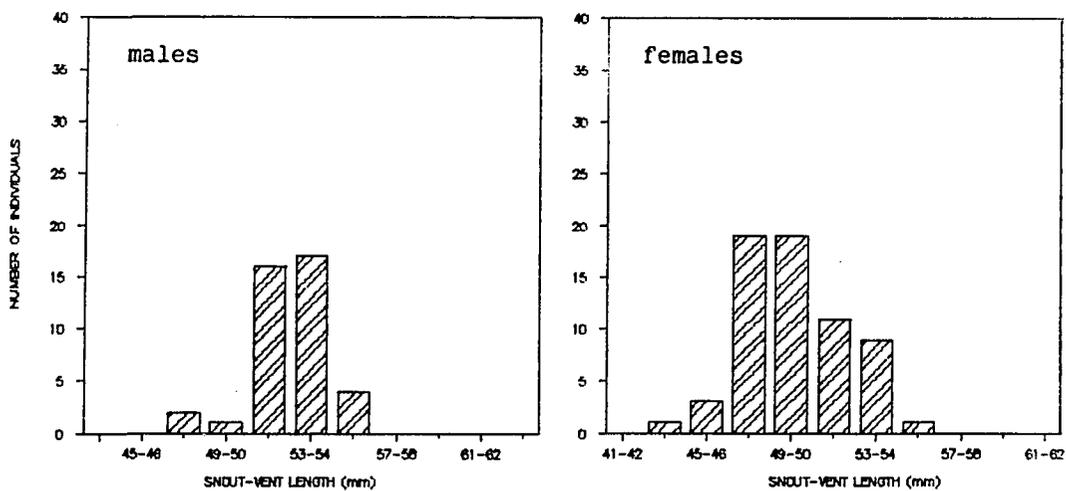


Fig. 4. Frequency distributions of snout-vent lengths of adult *Urosaurus ornatus* captured June 20 through September 30.

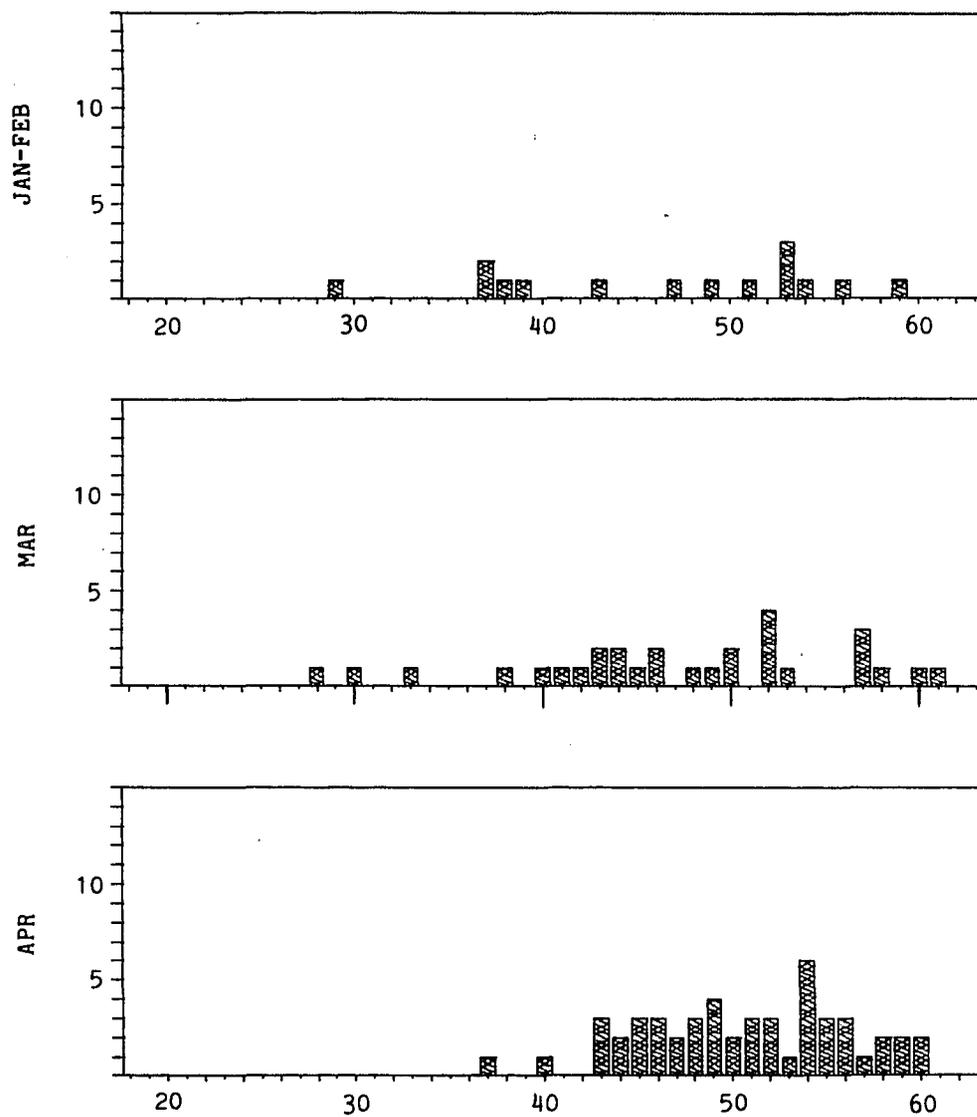


Fig. 5. Size frequency distributions of male Urosaurus ornatus at Tucson for each month indicated, giving number of captures on the vertical axis and mean snout-vent length (mm) on the horizontal axis.

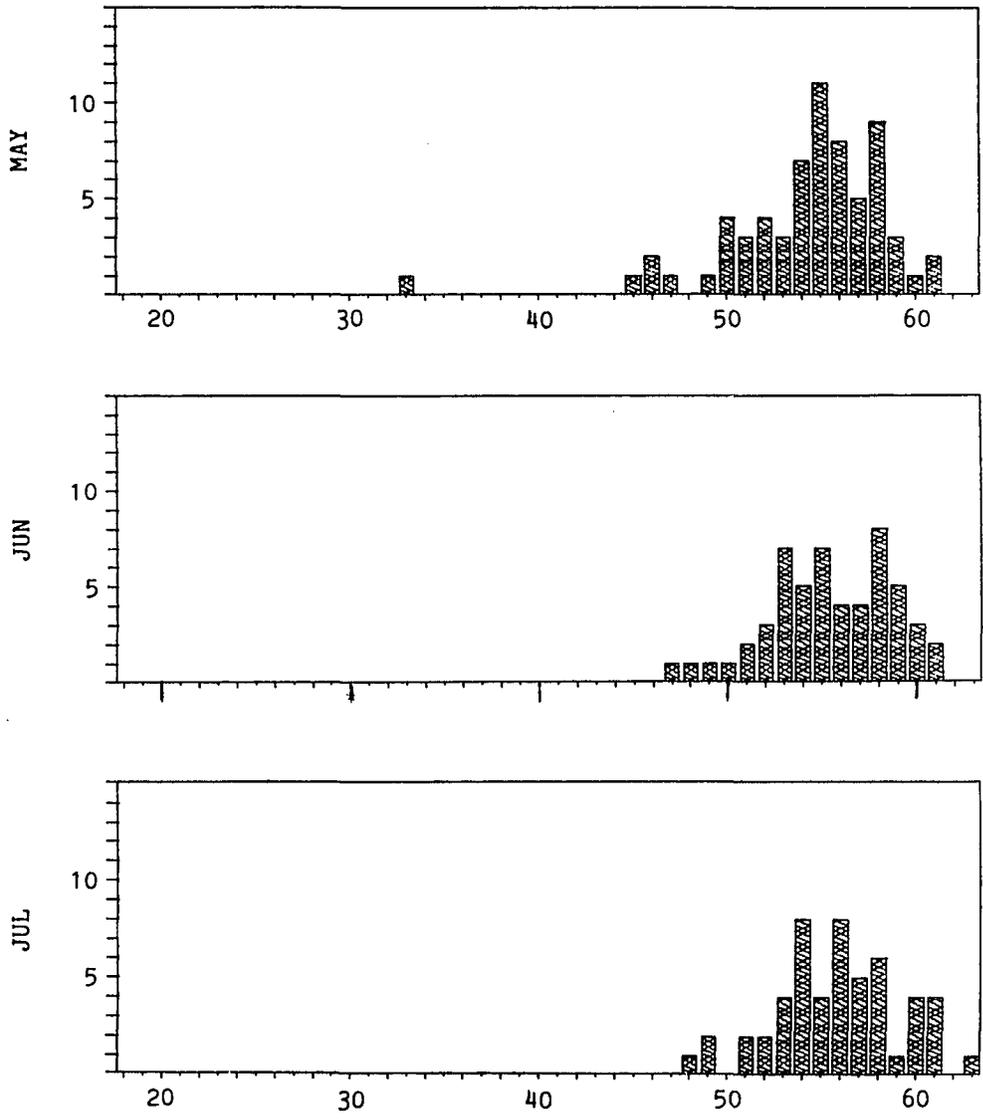


Fig. 5. --Continued

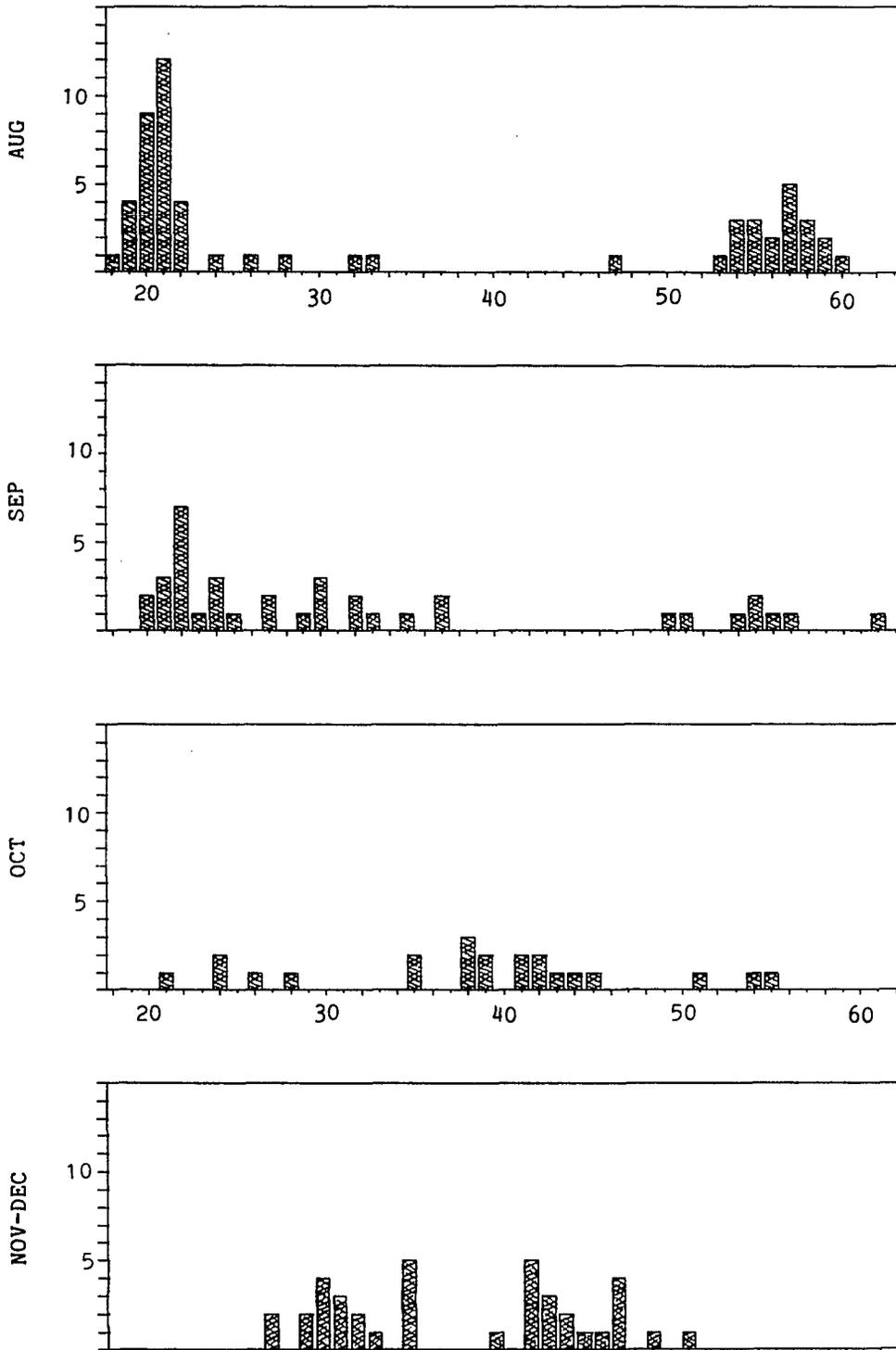


Fig. 5. --Continued

with umbilical scars collected at nest sites indicate a modal size of early hatchlings of 20 mm SVL with range of 18-22 mm. The absence of individuals less than 20 mm among later hatchlings may reflect a late season increase in hatchling size.

In March through May at Tucson, yearling male snout-vent lengths range from 28 to 59 mm, and yearling females from 28 to 49 mm. In June through August the ranges are 47 to 60 mm SVL and 47 to 52 mm SVL for first year males and females, respectively. Different hatching dates, local microhabitat variation in climate and food availability, and intrinsic individual factors such as initial mass, SVL, and growth rate should result in wide variations in the adult sizes attained. Furthermore, differential mortality and surface activity will influence observed size distributions. The relative contribution of each of these parameters is not known.

Differences Between Early and Late Hatching Offspring

Size records (SVL < 25 mm) of hatchlings in Figs. 6 and 7 indicate that there are at least two distinct hatching periods (modes) representing the first and second clutches produced by the majority of females. While there may be a third clutch laid by some females (<10%) during at least some years, there is only sufficient recapture data to fully verify a clutch frequency of two.

I assigned young-of-the-year to "early-hatching" or "late-hatching" groups based on the relationship between SVL and capture date illustrated in Figs. 6 and 7. Growth trajectories of frequently recaptured individuals, with at least some marked as hatchlings, permit construction of the dashed lines shown in Figs. 6 and 7. Assuming that

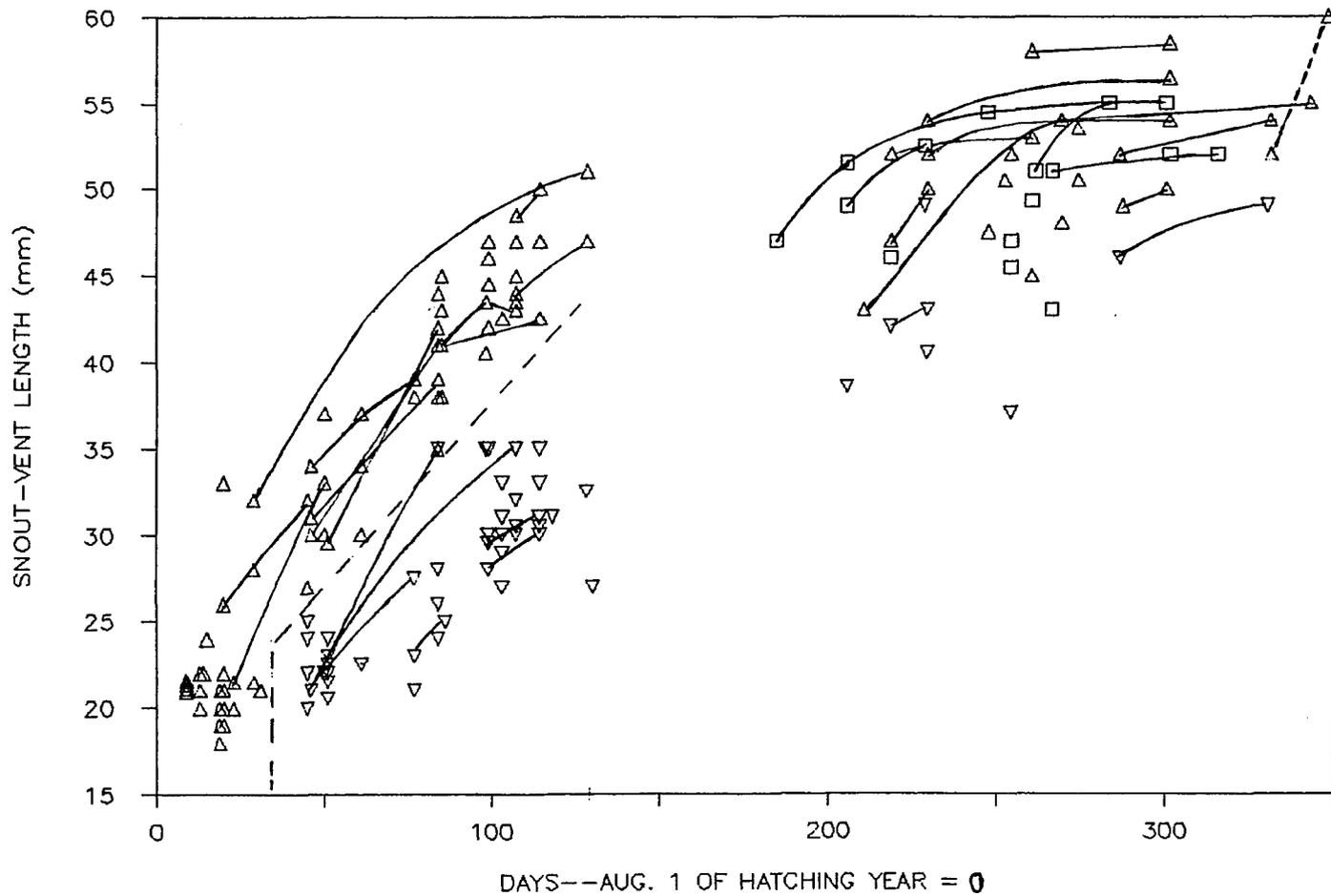


Fig. 6. Individual growth trajectories of male *Urosaurus ornatus* at Tucson. Up-triangles (Δ) for early hatchlings, down-triangles (∇) for late hatchlings, and squares (\square) for yearlings marked in January through April. Curves fitted by hand.

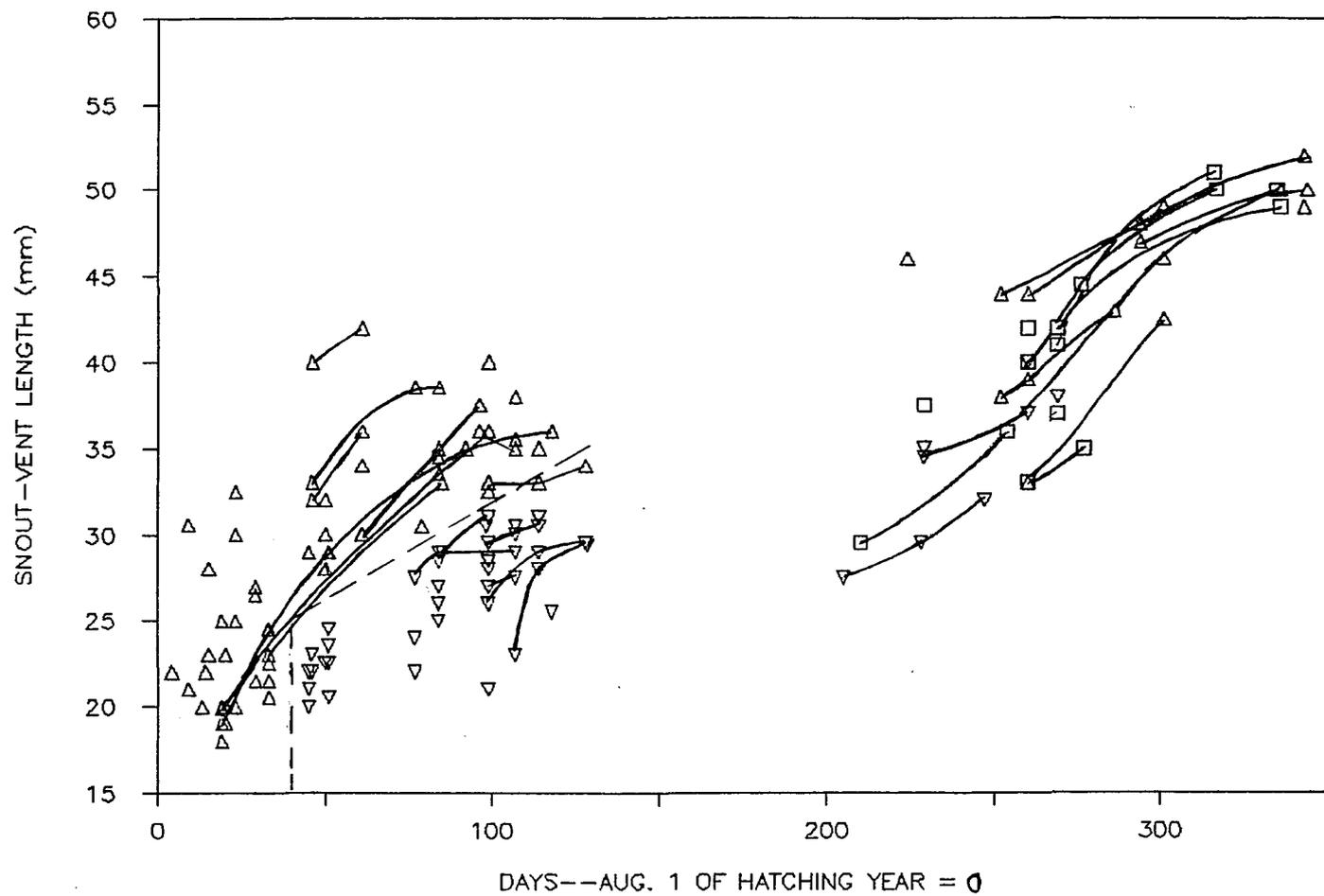


Fig. 7. Individual growth trajectories of female *Urosaurus ornatus* at Tucson. Up-triangles (Δ) for early hatchlings, down-triangles (∇) for late hatchlings, and squares (\square) for yearlings marked in January through April. Curves fitted by hand.

larger lizards, those falling to the left of (or above) the lines, hatched early, and smaller lizards, falling to the right of the boundary lines, hatched late, there is little subsequent overlap in the SVL between the two categories for recaptures shown in the figures.

In November-December, early-hatching males averaged a dramatic 13.7 mm greater SVL than late-hatching males ($t = 16.80$, $N = 45$, $P < .001$); see Fig. 6. Similarly, early-hatching females averaged a significant 7.1 mm greater SVL than late hatching females ($t = 8.76$, $N = 36$, $P < .001$); see Fig. 7. The largest late-hatching individuals recaptured in the following year are 49 mm and 40 mm SVL for males and females respectively, compared to 60 mm and 52 mm SVL for the largest early hatching males and females respectively. There are clearly fewer late-hatching yearlings in the populations.

Hatching time for the individual, i.e. from which brood (first, second, or third) a juvenile is derived, is an important factor in determining the neonate's relative growth and size, and therefore its eventual social status, mating success, or fecundity especially during the first breeding period following hatching. In the natural community, few yearling adults may survive to reproduce in subsequent years. This is to be explored in later sections.

Sexual Dimorphism

Sexual dimorphism in growth and size appears in the first fall season (ca 3 months after hatching). On the average, juvenile males are clearly reaching greater size than juvenile females by mid-November. Juvenile male captures exceed those of females. Relative surface activity (discussed in Part III) undoubtedly affects growth rates.

In Tucson, adult males average a significant 2.84 mm or 5.36% greater SVL than adult females ($t = 6.87$, $N = 227$, $P < .001$). At Agua Caliente the difference is 2.73 mm or 5.47% ($T = 6.15$, $N = 102$, $P < .001$). Data on mean adult SVL provided in Table 3 utilize individuals collected June 20 through Sept. 30 because late spring appears to be a period of high mortality, especially among first year males. It is desirable to have a sample that represents the potential breeding population. There is considerable sexual dimorphism in adult SVL in both populations. This observed pattern in sexual dimorphism could result not only from intrinsic differences in male and female growth, but also from a greater attrition of smaller first year males.

Sexual dimorphism in size and growth is common among lizards; males are generally larger than females. More than one factor may be contributing to the observed pattern of sexual dimorphism including differential allocation of resources to growth and reproduction, differential foraging, and sexual selection. Some saxicolous populations of Urosaurus ornatus studied in southern New Mexico and west Texas exhibit no sexual dimorphism in SVL (Zucker 1987).

Population Differences

A comparison of mean and maximum SVL between populations is equally striking as that between sexes. Adult males in Tucson average 3.13 mm or 5.94% greater in SVL than males at Agua Caliente ($t = 6.09$, $N = 128$, $P < .001$); likewise Tucson females average 3.02 mm or 6.05% greater in SVL than the females at Auga Caliente ($t = 6.90$, $N = 201$, $P < .001$). The difference in mean SVL between populations could be due

Table 3. Snout-vent lengths for all adult Urosaurus ornatus collected from June 20 to September 30 for all years combined.

	N	Mean SVL \pm SE (mm)	Range
Tucson Population			
Males	89	55.79 \pm 0.32	47.0 - 63.0
Females	138	52.95 \pm 0.26	42.0 - 62.0
Agua Caliente Population			
Males	39	52.66 \pm 0.26	47.5 - 56.0
Females	63	49.93 \pm 0.31	44.5 - 55.5

partly to different age structures, but such may not explain the difference in maximum size attained.

The largest male captured in the Tucson population was 63.0 mm in SVL compared to 56.0 mm for the largest Agua Caliente male. Nine of 89 (10.1%) of all Tucson males reached at least 60.0 mm in SVL; in the Agua Caliente population sample none exceed 56 mm in SVL. Moreover, Tucson males range to 60.0 mm in SVL in their first summer following hatching. Insect sticky trap data for one day in April reveal 278 insect captures at Tucson and only 7 captures at Agua Caliente. Although the data are for a one day sample, it suggests that food availability is greater at the irrigated Tucson (urban) study site.

The mean and maximum size of lizards at the Tucson site appears to be unusually high for the species throughout the remainder of its geographic range. Examination of 1,541 preserved (UAZ) specimens of U. ornatus, collected throughout Arizona and Sonora, Mexico provides an estimate of maximum size attained in the species. The largest males were selected and then measured. The 48 largest males out of 1541 lizards ranged in SVL from 53 to 59 mm with a mean of 54.7 ± 0.2 mm. Only 9 of these were greater than 55 mm SVL and the largest, 59 mm was from Phoenix, AZ.

Fairly large adult tree lizards have been reported by Vitt et al. (1981) and by Tinkle and Dunham (1983) with adults up to 60 mm and 58 mm (females only) respectively. Both of these studies were located in riparian habitats in south central Arizona. That of Vitt et al. (1981) was along the Verde and Salt rivers (at or below 1900 ft) that

flow most of the year. Most other reports on this species were from saxicolous populations or at higher elevations.

Growth

Growth rates vary between seasons, size and age classes, individuals, and populations. The growth rate of an organism is most simply described as change in length divided by change in time. It is accurately determined from growth interval data only if growth is nearly linear or the intervals are short. In many species, including Urosaurus ornatus, the initial phase of rapid juvenile growth is nearly linear, suddenly switching to much slower adult growth which is also nearly linear. The overall growth trajectory of size on time can be described as an asymptotic relationship with growth rate decreasing towards zero as the maximum or asymptotic size is approached. Body size attained is affected by the length of the growing periods as well as the growth rates.

Growth in the First Year

Juvenile growth is rapid (0.2 mm/day) in the late summer and fall as indicated by individual recapture data, where SVL is plotted on date (time in days) in Figs. 6 and 7. Growth rates are reduced to near-zero overwinter, from late November to early February at the Tucson site. During all winter months, in Tucson, a few individuals of all size classes were observed on warmer days in sunlit areas in this urban population. In sharp contrast no lizards were observed to be surface active in the natural habitat at Agua Caliente after November 19 on any year in this study.

Beginning in mid-September at both study sites in the Tucson region, mean daily high and low temperatures fall sharply; nocturnal lows are generally less than 19 °C. During the overwinter period mean daily high temperature falls below 20 °C and day length below 10.5 hours. Length of day and available sunshine are critical to thermoregulation and time available for foraging. Most January highs are in the range 15-20 °C, with the mean minimum between 1-6 °C.

Juveniles grew rapidly again in the spring. Males began leveling off later in the spring. Females continued to grow into the summer but stopped abruptly at or above 47 mm SVL in mid-July presumably to divert resources to egg development. Few females approach the large size attained by many males.

Growth in Adults

Most adult males and females gain additional length by a few mm in subsequent years. Many, however, show zero growth for several years, and a few of these show repeated tail loss (see below). SVLs of known aged adults at Tucson were regressed on age in years. These include only individuals at least 330 days (0.904 years) old, marked before May 1. August 1 of the hatching year is age zero. The data and results, presented in Fig. 8, estimate annual adult growth at 2.8 mm/year for males and 1.9 mm/year for females.

Regression equations (Fig. 8) were used to examine residual variation in SVL of early vs late hatching offspring two or more years old. Although most individuals in each class are of the appropriate hatching period, it is best to view them as larger vs smaller yearlings. The comparison of residual variation in SVL between the two groups is

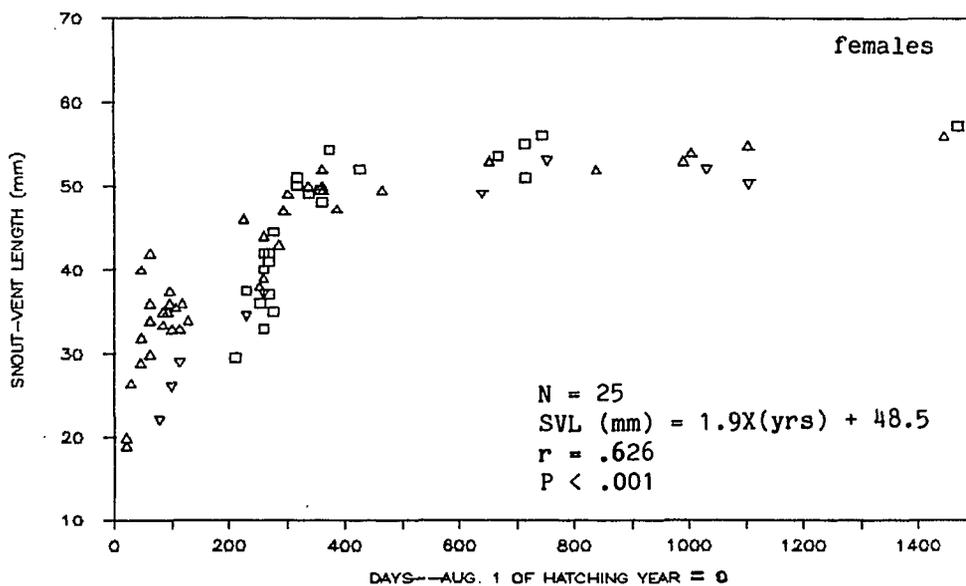
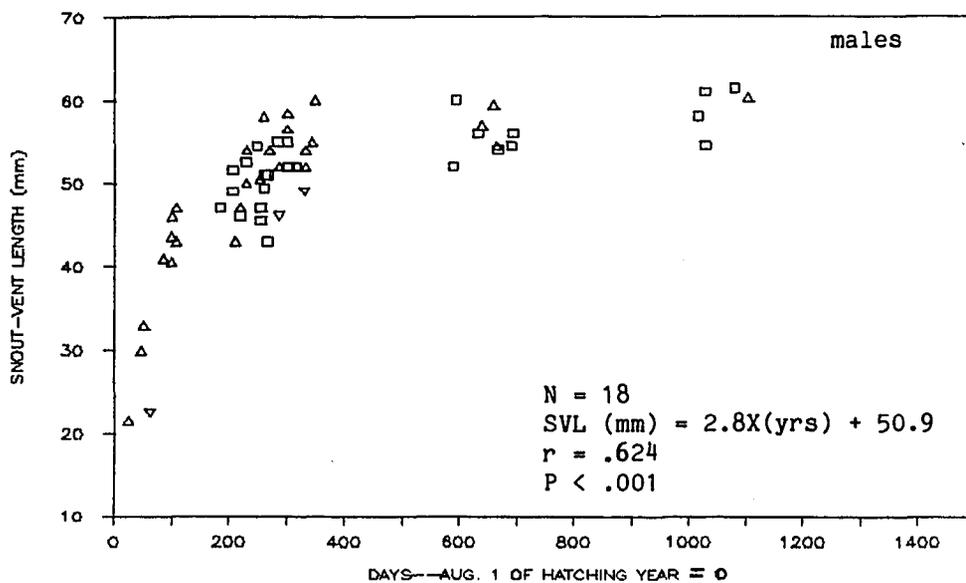


Fig. 8. Snout-vent length plotted on time of known aged Urosaurus ornatus at Tucson. Up-triangles (Δ) for early hatchlings, down-triangles (∇) for late hatchlings, and squares (\square) for yearlings marked in January through April. Regression equations provided for adults 330 days or later, averaged once per year.

marginally significant for Tucson females ($t = 2.01$, $N = 22$, $P = .07$). Larger yearlings, mostly early hatching offspring, average larger in SVL than smaller yearlings, throughout life. Too few smaller or later hatching males were recovered after one year to make a similar analysis.

Effects of Tail Loss

A comparison of individuals with complete tails to those undergoing regeneration indicates, with rare exceptions, no apparent effect of tail-loss on growth rate. Some individuals suffer repeated tail loss that may retard growth. One Tucson male (#3) lost its tail at least three times in 13 months, and appeared slightly deformed.

Broken tail pieces were recovered and measured for four lizards in which the tail was broken in capture. Mean percent body mass loss and mean percent tail loss are 5.1% and 67.6% respectively ($N=4$). Losing only 5% of total mass with two-thirds of tail loss in Urosaurus ornatus is much less of a loss than Zweifel and Lowe (1966) reported for Xantusia vigilis, where growth following tail loss proved to be below average. Xantusia is a K-strategist (long lived, late maturing, females initiate reproduction in their third year of life) that stores more energy in its tail, whereas Urosaurus is an r-strategist (short lived, early maturing, females reproduce at less than one year of life) that cannot afford to divert much energy to a large tail.

Growth as a Function of Size

One approach to growth analysis involved the use of growth interval (recapture) data to examine the relationship between growth rate and SVL. This has been reported for other iguanid lizards including

Iguana iguana (Rand and Greene 1982, Harris 1982, and Van Devender 1982), Ctenosaura similis (Van Devender 1982), Basiliscus basiliscus (Van Devender 1978), Anolis (Schoener and Schoener 1978, and Trivers 1976), and Sceloporus merriami (Dunham 1978).

For Urosaurus ornatus this was performed on all recapture intervals exclusive of Nov 15 to Feb 15 (near-zero growth). Intervals less than 15 days were eliminated if they could not be combined with temporally adjacent intervals. The data, transformed to change in SVL (over duration in days) on mean SVL, are graphed in Fig. 9 for males and females, respectively, at Tucson.

Linear Analysis of Growth Rates.--Linear regression techniques were used to fit straight lines (not shown) to the data as graphed in Fig. 9, and to similar data for Agua Caliente. From the results, provided in table 4, it is clear that growth rate decreases with increasing SVL. Males initially grow faster than females. The relationship of growth rate to SVL is nearly linear in males while in females it appears somewhat flat for small and intermediate size classes, then decreases towards zero for animals of adult size. Consequently, the X intercept--or asymptotic SVL--as fit by linear regression is overestimated for females. The parameter estimates provided in Table 4 can be used to produce Von Bertalanffy growth equations. Nonlinear techniques are used to do this in the next section.

Nonlinear Analysis of Growth Rates.--With the aid of computer assistance, nonlinear least squares techniques were used to estimate

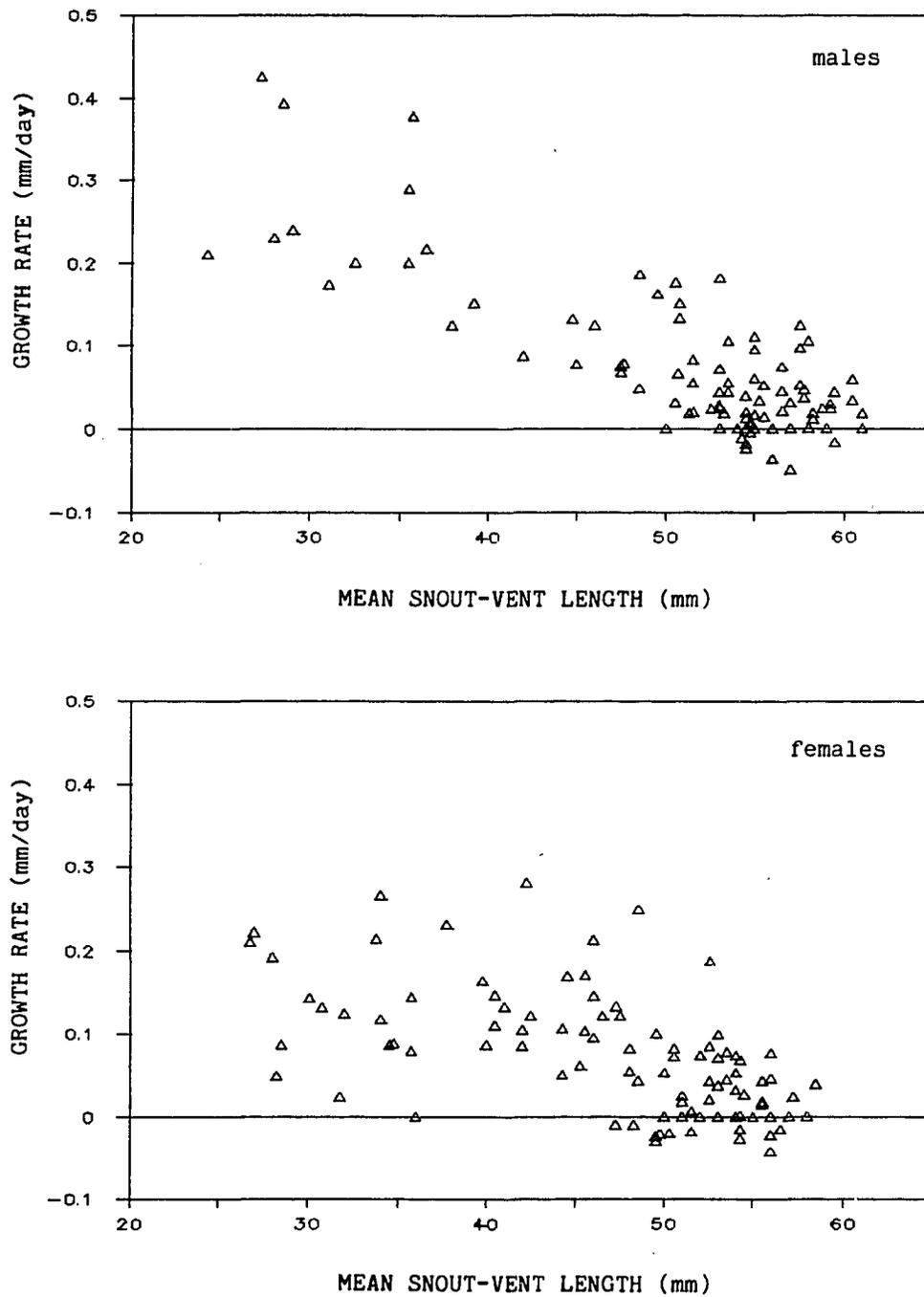


Fig. 9. Growth rate (difference in length / difference in time) plotted on mean snout-vent length for Urosaurus ornatus at Tucson.

parameters of growth interval equations using the same recapture data that produced Figs. 6 and 7. The analysis requires initial SVL, recapture SVL, and time in days; the same data that produced growth rate on mean SVL discussed above. Nonlinear regression uses initial SVL and time in days as two independent variables and recapture SVL as the dependent variable. The points plotted in Fig. 9, and to which the linear techniques were applied, represent a secondary data transformation by approximating the instantaneous growth rates from interval data and then using the mean as the independent variable.

A growth interval equation can be transformed into an equation providing growth rate ($dSVL/dt$) as a function of SVL and another providing SVL as a function of age. These are derived by Schoener and Schoener (1978) for the Von Bertalanffy, logistic-by-length, and logistic-by-weight, growth models used here. Logistic-by-weight is actually logistic-by-length³. Although body weight is subject to more diurnal variation than SVL³ and therefore preferred for this analysis, it also does not always vary exactly with SVL³ (see Table 2). The three forms (equations) for each model and the programming used for this analysis appear in Appendix A.

The methods do not require that individuals are of known age. For each model the parameters estimated are the asymptotic SVL (A) and the characteristic body growth rate (r). It is necessary to provide initial estimates of (A) and (r); the final values are then determined by iteration. The 95% "support plane" confidence intervals are calculated using the standard errors provided with the computer printout.

Table 4. Linear regression data reductions for Urosaurus ornatus recaptures where growth rate = $a + b(\text{SVL})$.

N	$r \pm \text{SE}$	$a \pm \text{SE}$	$b \pm \text{SE}$	$- a / b$
Tucson Males				
100	$- 0.82 \pm 0.05$	0.52 ± 0.03	$- 0.0088 \pm 0.0006$	59.09
Tucson Females				
105	$- 0.62 \pm 0.06$	0.33 ± 0.03	$- 0.0055 \pm 0.0007$	59.65
Agua Caliente Males				
30	$- 0.87 \pm 0.04$	0.61 ± 0.06	$- 0.0112 \pm 0.0012$	54.42
Agua Caliente Females				
31	$- 0.69 \pm 0.04$	0.43 ± 0.07	$- 0.0076 \pm 0.0015$	56.86

The model with the smallest SSQR/N is the best fit. This analysis tests the difference in growth increment data between sexes and between populations. Ideally it would also provide an age for every animal measured but such is not possible given the individual variation in growth in Urosaurus ornatus.

For the Tucson population, the results presented in Table 5 show a higher asymptotic SVL for males than for females. It is significant for both logistic models but not the Von Bertalanffy model. Larger values of (r) are consistently indicated for Tucson males, but none are significant. A larger (r) does, however, indicate that the asymptotic SVL is approached sooner which appears to be the case. Yearling males appear to level off in the spring, whereas females level off in the summer.

It is significant that male and female recapture data are fit best by different models; Von Bertalanffy and Logistic-by-length respectively. This is consistent with the picture in Fig. 9, however I offer no estimate of its significance. Although not significant, the higher estimates of asymptotic SVL, consistently predicted (Table 5) for Agua Caliente females over males, do not agree with the previously established pattern of sexual dimorphism. An under-representation of juvenile recaptures in the Agua Caliente could add considerable error to the parameter estimation.

While there are less data for smaller sized individuals, especially at Agua Caliente, late-hatching juveniles do show lower growth rates than early-hatching juveniles for both males and females. Von Bertalanffy and logistic-by-length growth equations (Table 5,

Table 5. Nonlinear regression data reductions of growth interval data.

SSQR/N = residual sum squares / sample size, A = asymptotic SVL, r = characteristic growth rate

	SSQR/N	A \pm 95% CI (mm)	r \pm 95% CI
Tucson Males			
N = 100			
Von Bertalanffy	2.98	57.8 \pm 1.4	0.0098 \pm 0.0018
Logistic by Length	3.62	56.8 \pm 1.1	0.0174 \pm 0.0030
Logistic by Weight	4.70	56.4 \pm 1.0	0.0264 \pm 0.0055
Tucson Females			
N = 105			
Von Bertalanffy	4.15	55.3 \pm 1.9	0.0084 \pm 0.0018
Logistic by Length	3.97	54.3 \pm 1.2	0.0142 \pm 0.0023
Logistic by Weight	4.48	53.9 \pm 1.0	0.0209 \pm 0.0033
Agua Caliente Males			
N = 30			
Von Bertalanffy	1.11	53.4 \pm 1.3	0.0140 \pm 0.0044
Logistic by Length	1.04	53.3 \pm 1.0	0.0193 \pm 0.0053
Logistic by Weight	1.07	53.3 \pm 0.9	0.0251 \pm 0.0067
Agua Caliente Females			
N = 31			
Von Bertalanffy	2.14	56.1 \pm 4.2	0.0080 \pm 0.0037
Logistic by Length	1.82	54.6 \pm 2.5	0.0124 \pm 0.0019
Logistic by Weight	1.69	53.9 \pm 1.9	0.0170 \pm 0.0048

Appendix A) for Tucson males and females respectively, permit a comparison of residual variation in recapture SVL (L_2) between early- and late-hatching offspring. Recaptured early hatching offspring average significantly larger than recaptured late hatching offspring ($t = 2.4$, $N = 39$, $P < .05$), based on the difference between expected and observed L_2 .

It cannot be determined if depressed second clutch growth rate is caused in greatest degree by peer-pressure from the now larger first clutch juveniles, or by the declining nocturnal environmental temperatures later in the season when most late-hatching captures are recorded. Experimental removal of first clutch offspring from designated plots should resolve part of this question.

For each model there is a form that provides SVL as a function of age. These equations do not compensate for the overwinter period of inactivity or other seasonal influences on growth, whether climatic or biological. Even if the winter seasonal effects were eliminated, the models would not accurately predict the mean SVL for a given age. Beyond the first year of life they predict additional growth of less than one percent yet the recapture data show that many adult lizards undergo significantly greater growth.

Patterns of Variation in Lizard Growth

Results of previous growth studies of lizards have also demonstrated that males generally grow faster than females and achieve a larger adult size. Males and females apparently do not differ in the characteristic growth rate (r), but do so significantly in the asymptotic SVL (A) thereby producing different absolute growth rates

(Schoener and Schoener 1978, and Dunham 1978). Growth rates have been shown to be positively correlated with precipitation and food abundance (Zweifel and Lowe 1966, Andrews 1976, Ballinger 1977, Dunham 1978, and Licht 1974). It should be expected that both (r) and (A) increase with food abundance but there was no change in (A) reported by Dunham (1978) for Sceloporus merriami when (r) varied considerably. The results of Schoener and Schoener (1978) are similar but temperature and population density cannot be ruled out as factors.

It would be interesting to compare growth in the second year of life of lizards with supplemented diets where one sample was provided with unlimited food in the first year and the other deprived of substantial growth in the first year of life. In other words, would smaller individuals "catch up" or get farther behind? It is common knowledge among zookeepers that hatchling reptiles of a given cohort reared to maturity achieve widely disparate body sizes when some are fed significantly less than others. Heloderma suspectum with stunted growth (half ration) reach a maximum size well below the average for the species and for captives on full ration; they are otherwise reproductively mature (Lowe, pers. comm.).

When adult survival is high and competition for territories intense, juveniles would be better off delaying maturity and prolonging growth (Ferguson and Brockman 1980). Male basilisks studied by Van Devender (1978) show no seasonal variation in growth, however, females have reduced growth rates during the drier periods suggesting to him that food may at one time be superabundant for males and limited for reproductive females. Interestingly, males show prolonged growth and

higher (A) where the adult sex ratio is less in favor of females. It would be valuable to determine if a developing individual is capable of a facultative switching of growth strategies. Gates (1963) had suggested a similar effect of the demographic environment on the development of throat color in Urosaurus graciosus.

Summary of Part I

Adult males of Urosaurus ornatus reach larger body size than adult females. Males average 55.79 ± 0.32 mm and females, 52.95 ± 0.26 mm at Tucson. Individuals of the Tucson population (urban) average much larger in body length than those at Agua Caliente (desert) for any age group more than four months after hatching. Males average 52.66 ± 0.26 mm and females, 49.93 ± 0.31 mm at Agua Caliente. Maximum snout-vent length and weight at Tucson are 63.0 mm and 8.45 g; at Agua Caliente, 56.0 mm and 5.40 g. This difference is attributed to extended activity and growth seasons and to greater longevity at Tucson. Degree of sexual size dimorphism is the same for both populations.

At least some variation in body size, resulting from environmental conditions affecting growth in the first year, is retained throughout life. Earlier-hatching offspring (first clutch) are larger than later-hatching offspring (second or third clutch) throughout life. There are no hatchlings of 18 and 19 mm SVL in the later-hatching group suggesting a possible increase in hatchling size later in the season.

In U. ornatus, growth rates decline during winter inactivity, gradually with increasing SVL, and more abruptly at the onset of reproductive activity. Growth data for males at Tucson is fit best by a

von Bertalanffy curve while growth data for females is fit best by a logistic-by-length curve. This may reflect actual differences in the growth programs of the sexes. The majority of individuals, male and female, continue to grow at least an additional five percent in SVL after their first adult year; more than predicted by either logistic or Von Bertalanffy models. The (phenotypic) data are subject to many sources of variation (hatching date, climate, predation, etc) that should be experimentally tested in future investigations before the significance of each to the life history of Urosaurus ornatus can be resolved.

RESULTS AND DISCUSSION

PART II. DEMOGRAPHY

Preliminary observations of the two populations of U. ornatus investigated in this study indicated that the Tucson population has greater mean and maximum body sizes of lizards than the Agua Caliente population. Much of this body size difference, between the two populations, analyzed in the previous section, is undoubtedly the result of environmental conditions more favorable to growth at Tucson. It was also hypothesized that some body size difference results from differences in age structure with a greater proportion of older adults in the Tucson population. Relationships between body size, fecundity, mortality, and environment are explored in this section.

The recapture data show real differences in age structure and survivorship between the two populations. At Tucson, yearling adults account for approximately 50 percent of the summer population compared to a more typical 72 percent at Agua Caliente. Greater longevity and body size at Tucson are expected to result in higher population density, greater fecundity, and reduced juvenile survivorship. Also, density-dependent mechanisms are expected to play a proportionately greater role in regulating the Tucson population.

Population Density

Tucson and Agua Caliente population study areas are 1.4 and 1.6 ha respectively. Comparison of densities between the two populations

for the summer of 1979 reveals 116 lizards/ha at Tucson and 48 lizards/ha at Agua Caliente, based on Lincoln-Petersen Index estimates (Table 6). The values may tend to underestimate population size because the structural habitat does not permit equal observer accessibility to all individuals. For consistency, nine females were excluded from the 1979 Tucson precensus because they were marked during intensive observation of nesting females concentrated at the Main Gate nesting area.

Longevity

Of the lizards marked in the Tucson population, fourteen were last collected in at least their third year of life, three in at least their fourth, and one was last seen in its fifth year. The oldest known female (#39) was marked as a juvenile in April 1979 and last collected in May 1983. Having hatched in 1978 it would be four years old by the birthday rule, and be in its sixth calendar year and about to begin its fifth summer as an adult. The oldest male (#44) was marked as an unknown aged adult in April 1979 and last recorded in March 1982.

At Agua Caliente six lizards were last captured in at least their second year and only one in at least its third year of life. Lizards are much more difficult to recover at Agua Caliente and it is presumed that they may well live longer than four years. While the overall picture suggests that maximum longevity is at least five years in this species, few or none reach that age in the completely wild population studied.

Table 6. Lincoln-Petersen Index estimates of population size at Tucson and Agua Caliente.

$N = Mn/m$ estimated population size, M = number marked in first census, m = number of recaptures in second census, n = total captures in second census

M	First Census	m/n	Second Census	N	<u>±</u> SE
Tucson 1979					
103	(Jun 11 - Jul 20)	19/30	(Jul 24 - Nov 26)	162.6	<u>±</u> 20.4
Tucson 1980					
81	(Jun 10 - Aug 4)	21/30	(Aug 14 - Sept 20)	115.7	<u>±</u> 12.0
Agua Caliente 1979					
35	(Jun 16 - 18)	15/33	(Jul 24 - Sept 16)	77.0	<u>±</u> 11.2

Survivorship

Survivorship is estimated from adult age class structure, by measuring the size of a cohort at different ages, by measuring the survivorship rates of each age class from the percent recaptured, and by inferring mortality from estimates of egg production. Each of these requires that assumptions be made about the population or the sampling which are often violated in practice. The methodological variation in this study (see below) as well as throughout the literature should be considered when making comparisons.

Estimating survivorship in natural populations is subject to many well known sources of error. Some of these are more obvious: subgroups of a population often differ in their probability of capture (as in nesting females), sample sizes are often small, and animals not recaptured may be incorrectly assumed dead. Anything less than 100% recapture success of all living individuals will result in survivorship being underestimated. Such is evident by the number of lizards not recaptured the following census period but perhaps two or more later. Lincoln-Petersen Index (LPI) methods can be applied to recapture data to provide an estimate of survivorship without capturing all individuals. The data also include individuals marked in the spring, which must exclude larger yearlings (Males > 51 mm SVL, Females > 48 mm SVL) not distinguishable from unknown aged adults.

Survivorship at Tucson

The age structure of adults is evaluated on a case by case basis. In order to make use of all information on longevity, I included male (#44) in the following analysis. Otherwise, all other lizards,

used below, are of known age as determined from the recapture data. I used the LPI to correct an estimate of adult survival for 1979 to 1980, and the small-sample version of the LPI to estimate the sizes of cohort age classes for the first year of life. Survivorship curves of males and females for the first year of life are derived by imposing the cumulative sex ratios--from percent recaptured--on the series of cohort sizes estimated by LPI. Variation in survivorship is evident between sexes, early and late hatching offspring, different parts of the study area, populations, and different age classes.

Adult Survivorship.--Annual survival is estimated for adults by counting each individual as present for each year before it is last recorded excluding individuals that could not have been recovered further for various reasons (e.g. the study ended). Table 7 provides the results for each adult year class. The estimates of average annual adult survivorship are 21/43 (48.8%) for males and 30/56 (53.6%) for females.

In a different analysis, annual adult survival from 1979 to 1980 was determined by LPI for adults of all ages combined. In Table 6 only 34/103 (33.0%) of the lizards marked in the 1979 precensus period are recovered in the 1980 precensus period. Division of 34/103 by the fraction (21/30) of lizards recovered in the 1980 second census provides a corrected estimate. The result estimates adult survivorship at 47.2 percent; not dramatically different from that provided above. The overall estimates of population size for 1979 and 1980 in Table 6 show a decrease despite what is to be high adult survivorship for this species.

Table 7. Annual survivorship data for adult U. ornatus at Tucson and Agua Caliente, giving fraction and percent surviving for all years combined.

Age Class (years)	Tucson Population			Agua Caliente
	Males	Females	M + F	M + F
1	14/23 (60.9)	18/30 (60.0)	32/53 (60.4)	7/20 (35.0)
2	6/14 (42.5)	8/17 (47.0)	14/31 (45.2)	1/7 (14.3)
3	1/5 (20.0)	3/6 (50.0)	4/11 (36.4)	0/0 ----
4	0/1 (0.0)	1/2 (50.0)	1/3 (33.3)	
5		0/1 (0.0)	0/1 (0.0)	
Mean	21/43 (48.8)	30/56 (53.6)	51/99 (51.5)	8/27 (29.6)

The immediate implication is that recruitment was very low into the 1980 population.

Survivorship in the First Year of Life.--For the purpose of constructing survivorship curves and life tables, age classes are defined as follows: Hatchlings are all lizards measuring 18 - 25 mm SVL. Juveniles are young-of-the-year recorded before December 31, measuring at least 30 mm SVL (males) or 29 mm SVL (females); smaller juveniles are excluded to avoid excessive variance in age. Subadults are lizards less than one year old, recorded from January 1 to June 20. Due to variation in hatching date, the hatchling and juvenile age classes are distinguished by SVL. Estimates of cohort age class sizes, presented in Table 8, will provide a basis for determining survivorship.

Survivorship Curves.--In a population with a skewed sex ratio, it is desirable to have separate estimates of survivorship for each sex. I examined the percent recaptured for each age class and sex to produce a cumulative sex ratio, in Table 9, that can be used with the cohort age class information, adult survival, and egg survival (below) to prepare separate survivorship curves for each sex. These curves appear in Fig. 10 for both regular and semilogarithmic images.

Sexual Differences in Survivorship.--At Tucson, survival from egg to adult is 4.8% and 7.6% for males and females respectively. The greatest difference in male and female mortality appears to occur from spring to summer in the year following hatching. A comparison of subadult male and female survivorship data, provided in Table 9, is not significant ($\chi^2 = 1.03$, $P > .25$). Using the February to July survivorship values in Table 10 (below) does reveal a significant

Table 8. Lincoln-Petersen Index estimates of age class sizes at Tucson.

Age Class	Year of Hatching				Weighted Mean
	Estimate and (weighting factor) ¹				
	1978	1979	1980	1981	
Hatchling	--	327.0 (40)	178.7 (48)	265.4 (73)	254.9
Juvenile	--	50.8 (26)	139.0 (34)	114.1 (33)	105.5
Subadult	44.5 (21)	28.3 (21)	37.8 (7)	33.0 (8)	36.1
Adult 1yr	25.7 (14)	32.3 (4)	--	--	27.2

1. Weighting factor--number of lizards captured in the second census.

Table 9. Sexual differences in survivorship giving fraction of marked individuals recovered, percent recovered, and the cumulative proportions of males and females at Tucson.

	Hatchling	Juvenile	Subadult	Yearling Adult	Older Adult
Males					
Recap/marked	7/44	18/46	18/58	18/34	--
% Recovered	15.9	39.1	31.0	52.9	--
Proportion	50.0	48.2	46.0	38.6	39.9
Females					
Recap/marked	7/41	12/28	24/57	22/44	--
% Recovered	17.1	42.9	42.1	50.0	--
Proportion	50.0	51.8	54.0	61.4	60.1

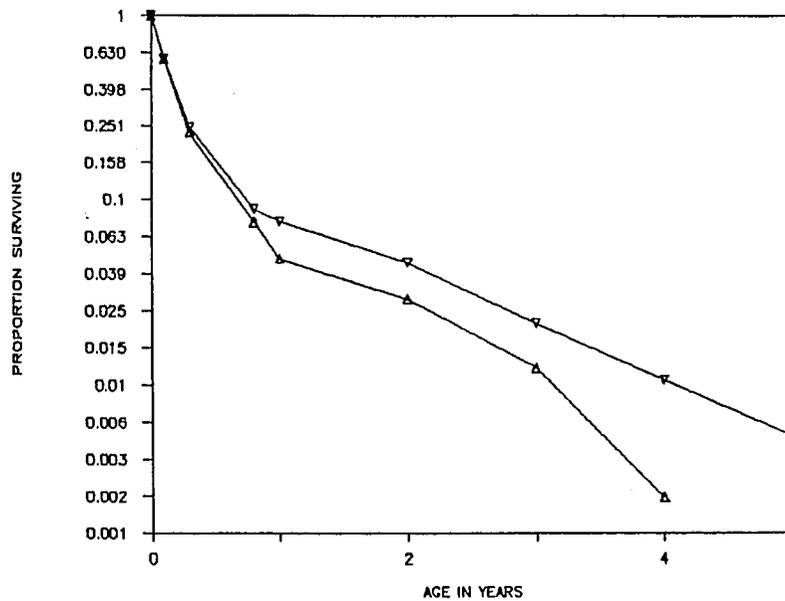
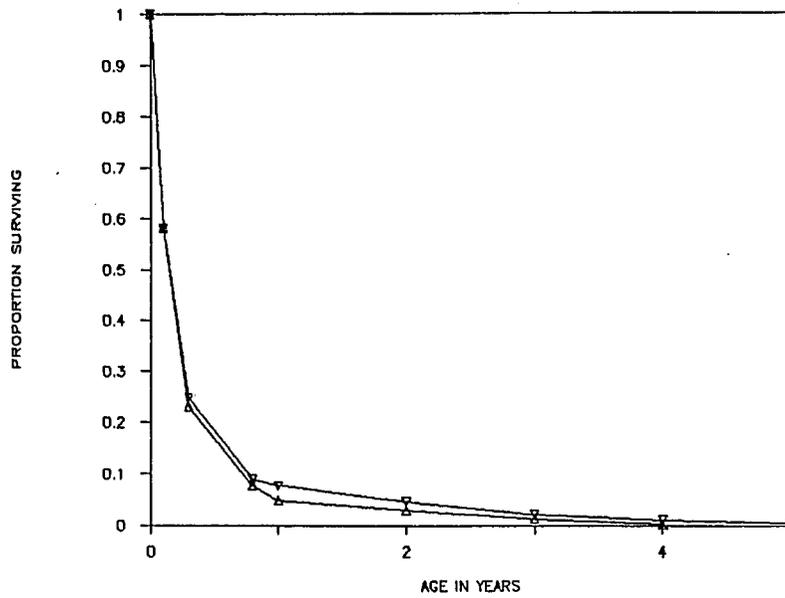


Fig. 10. Survivorship curves of male and female Urosaurus ornatus at Tucson; up-triangles (Δ) for males and down-triangles (∇) for females.

difference in survivorship between males and females ($\chi^2 = 3.75$, $P \approx .05$).

The adult sex ratios determined from Table 3 are 1.55:1 for F:M at Tucson, and 1.31:1 for F:M at Agua Caliente. Both are significant (Tucson-- $Z = 3.25$, $P < .01$; A.C.-- $Z = 2.38$, $P < .05$). Other populations of U. ornatus may show a skewed adult sex ratio favoring females. It is likely that the mortality rate of subadult males is dependent on both behavior and density. This is discussed in Part III.

Survivorship of Early- vs. Late-Hatching Offspring.--It has been demonstrated in Part I that the later hatching offspring are generally smaller than those of earlier broods, especially for the first year of life. Of significance to the life history of U. ornatus is the reduced survivorship in the late hatching group as indicated in Table 10 and Fig. 11. The two samples, early and late offspring, include all hatchlings or juveniles marked in the fall that were recaptured the following January or later. Individuals are counted as present in each month before last captured.

The difference in survival between early and late hatch is only significant among males from March to April ($\chi^2 = 5.97$, $P < .05$). This is precisely the period of most intense agonistic behavior among male tree lizards. Adult females are strikingly inconspicuous at this time. Undoubtedly, size plays an important role in survivorship of males.

Variation in Survivorship Between Habitats.--Hatchling survival at Main Gate is significantly lower than the remaining sample despite the large number of females nesting there ($\chi^2 = 4.35$, $P < .05$). Only 2/39 (5.1%) of the hatchlings were recaptured at the Main Gate area

Table 10. Comparative survivorship of early- and late-hatching lizards by month at Tucson. Lizards counted present each month before last capture.

Month	Males				Females			
	Early		Late		Early		Late	
	N	%	N	%	N	%	N	%
Jan	14	100.0	6	100.0	12	100.0	5	100.0
Feb	14	100.0	6	100.0	12	100.0	5	100.0
March	14	100.0	5	83.3	12	100.0	5	100.0
April	14	100.0	2	33.3	12	100.0	4	80.0
May	9	64.3	1	16.7	12	100.0	2	40.0
June	7	50.0	1	16.7	9	75.0	2	40.0
July	6	42.9	0	0.0	9	75.0	2	40.0
Aug	4	28.6			8	66.7	2	40.0
Sept	4	28.6			6	50.0	2	40.0
Oct	4	28.6			5	41.7	2	40.0
Nov	4	28.6			5	41.7	2	40.0
Dec	4	28.6			4	33.3	2	40.0

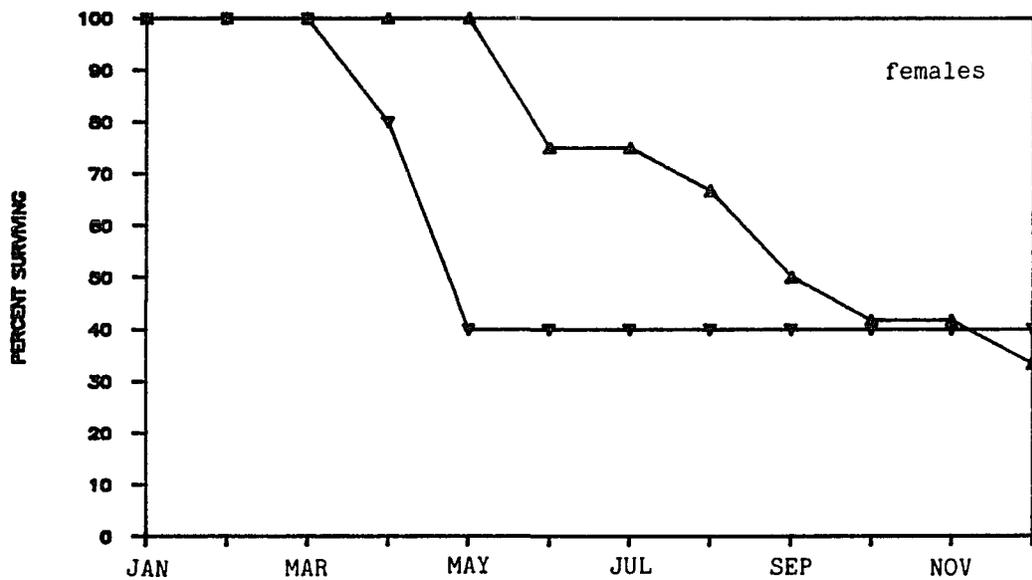
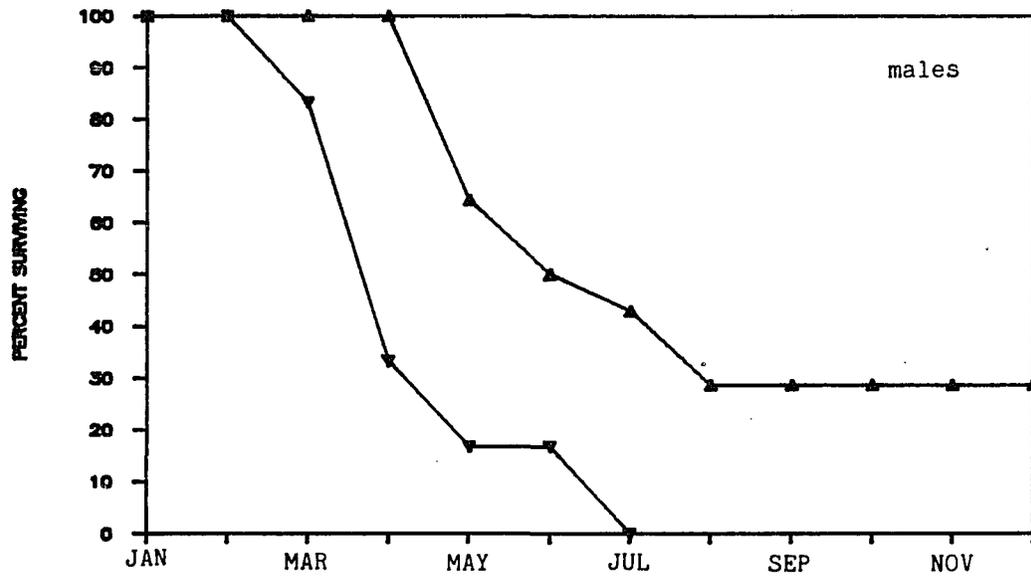


Fig. 11. Survivorship curves comparing early- and late-hatching offspring at Tucson. Up-triangles (Δ) for early-hatching and down-triangles (∇) for late hatching offspring.

compared to 11/42 (26.2%) of the hatchlings in the remaining areas. The Main Gate area has the highest human utilization on the study site and the stone walls there lack crevices or other potential refuge.

Survivorship at Agua Caliente

The method for Tucson adults given above is used to evaluate the composition of known aged adults at Agua Caliente, providing an estimate of annual adult survivorship for males and females combined. The size frequency distribution of females is also examined for comparison to the estimate of annual survival. Survival from egg to adult is further estimated by assuming a population replacement rate (R_0) of 1.0, and using the data for adult survival and egg production.

I considered Agua Caliente lizards to be of determinable age (less than one year old) if they measured no more than 49 mm SVL for males and no more than 46 mm SVL for females. Estimates of annual adult survivorship based on the age composition of age determined lizards (Table 7 above) indicate a mean annual adult survival rate of 29.6%.

Mean SVL of known first year adult females recaptured in the summer is 48.6 mm (46.5 - 50.0, N = 10). If those females greater than 51 mm SVL are older than their first year of adulthood, then 19/70 (27.1%) is an estimate of the proportion of older adults and the average annual adult survival.

It is possible to estimate minimum survival of females from egg to adult by estimating the number of eggs produced and the observed proportion of yearling females. Egg production is estimated from regression to be 15.0 per season for first year adults and 17.2 per season for older adults. Late appearance of hatchlings suggests up to

three clutches but with fewer than 10% of the females producing a third clutch. I assumed reproductivity of two clutches per female and used 27.1% as the estimate of annual adult female survivorship. The resulting estimate of prereproductive survivorship (egg to adult) is 9.4%.

Differences in Survivorship Between Populations

Average annual adult survival at Agua Caliente 29.6% (Table 7) is only marginally significantly different from the corresponding estimate for Tucson males and females combined (51.5%) ($\chi^2 = 3.25$, $.05 < P < .1$). Estimates of annual survivorship in other studies of Urosaurus ornatus are given by Dunham (1982), Tinkle and Dunham (1983), and Ballinger (1984). The total ranges reported are 1% to 25% for juveniles and 12.5% to 50.0% for adults. Typically the means reported are 7% to 12% for juveniles and 23% to 33% for adults.

This general pattern is quite similar to the natural population at Agua Caliente with juvenile survivorship at 9.4% and annual adult survivorship at 27.1%. In the urban population at Tucson, however, observed juvenile survivorship is less, at 4.8% and 7.6%, for males and females, and adult survivorship is greater, at 48.8% and 50.0% for males and females respectively. Although within the range of previous reports, the low first-year survivorship values reported for this urban population may reflect greater habitat saturation, and consequent density-dependent mortality of juveniles.

Mortality

Based on survivorship data for Tucson males and females, the mortality curve for this species would appear U-shaped with one-year-olds enjoying the lowest mortality rate. Adult mortality rates may actually be relatively constant. The difference in mortality rate between first year and older adults is not significant from the results in Table 7 ($\chi^2 = 2.86$, $.05 < P < .1$).

Seasonal variation in mortality is also evident. The ages and dates of high mortality can be difficult to establish. If a survivorship curve indicates a sharp decline, based on the number of lizards last seen, one cannot be sure if mortality occurs then or during a period of reduced sampling (e.g. overwinter) that follows.

Adult females clearly reach a minimum fat-body weight in August, in other populations reported by Michel (1976) and Ballinger (1977). While this is neither unexpected nor unusual, it may indicate a period of greater resource stress on females following reproduction. There is a three to one ratio of adult females over adult males active in September through November, suggesting the expected greater need for postreproductive foraging by females.

Competition, aggressive behavior, reproduction, and drought may cause stress and exposure. Freezing and predation are the only documented factors contributing directly to mortality. Mortality due to freezing was observed at Agua Caliente in a previous study in 1959 - 1961 by C. H. Lowe and J. W. Tremor. Occasional (up to 3) dead lizards were uncovered in small peripheral aggregations more shallowly located inside of mesquite limb-trunk junctures. No dead lizards were found in

the larger main aggregations deeper in the wood, totaling 27 in one mesquite and 31 in another. In another study, Vitt (1974) observed two aggregations of U. ornatus with 155 individuals, mostly under the bark of mesquite trees. Two other peripheral aggregations produced 13 lizards, all dead. Among winter aggregations in Texas, Worthington and Sabath (1966) found six of 125 U. ornatus dead.

Actual predation on young tree lizards by passerine birds was observed twice at Tucson in the spring. Actively foraging lizard-eating snakes were observed at Agua Caliente. Snakes may eat a greater proportion of larger lizards. At Tucson, there has been a potential for predation by humans and a large number of feral cats; it is, however, likely that predation is more intense at Agua Caliente due to the greater abundance and diversity of lizard predator taxa observed there. An experienced adult tree lizard in an optimal home range is safer from predation at Tucson just from the absence of snakes alone (see Table 1).

Reproduction

Reproductive Cycle

Data on the histological and temporal aspects of reproduction in Urosaurus ornatus are provided by Asplund and Lowe 1964, Parker 1973, Michel 1976, Van Loben Sels 1976, Martin 1977, Tinkle and Dunham 1983, and others. Many studies on U. ornatus provide seasonal data on the occurrence of gravid females and the appearance of hatchlings. The former varies in definition and in this study refers to the condition detectable from a live animal held in the hand. Ideally such data are obtained by x-ray.

In this study, in southeastern Arizona, hatchlings did not appear until late-July. Hatchlings are reported as early as mid-June in central Arizona by Tinkle and Dunham (1983), and late-June in central Texas by Martin (1977). These fairly wide population timing differences are likely the result of combined regional climate coupled to base elevation, and more local environmental factors also affecting soil microclimate and productivity.

Gravid females were noted in June, July, and August. Percent of females in gravid condition is provided in Table 11 for each two week period of the summer (all years combined). Given the first appearances (Tucson site) of gravid females (June 10), oviposition (July 2), and hatchlings (August 4), it should follow that gravid females in late-August will produce late-October hatchlings. The latest observation of hatchling sized lizards in the field are 21mm SVL on November 7 and 23mm SVL on November 15, 1981. Mean incubation period of eggs at constant 28 °C, laid and hatched in the laboratory, is 29.3 days (28 - 32, N = 3 clutches).

Nesting Patterns

Oviposition is characterized by nest site selection that generally takes the female out of its home range. During the months of July and August gravid and post-partum females are frequently encountered on the ground often with "mud balls" under their claws. Sometimes much of the body is covered with dry soil. This period obviously poses an added risk by exposing the female lizard to terrestrial predators. At Tucson most females recaptured on successive years remained in the same area. Two females (101 and 106) returned to

Table 11. Occurrence of gravid female U. ornatus at Tucson for all years.

Time Period	Number of Captures	Percent Gravid
May	67	0.0
June 1 - June 15	24	58.3
June 16 - June 30	33	90.9
July 1 - July 15	60	66.7
July 16 - July 31	34	61.8
Aug 1 - Aug 15	27	70.7
Aug 16 - Aug 31	13	23.1
September	19	0.0

their home trees after nesting at sites along a stone wall at distances of 48 m and 40 m respectively. Due to the particular distribution of soil suitable for nesting at the Tucson urban site, this unusual pattern of migration to oviposition sites is not unexpected. At Saguaro National Monument (east of Tucson), M`Closkey, Baia, and Russel (1987) concluded that home ranges of female U. ornatus include nest sites at the bases of occupied trees, confirming that oviposition outside of the home range is unusual for this sedentary species. It is not known to what extent Tucson females have difficulty if any in relocating their original home ranges (from the data it is assumed they have little or none).

Nest Location and Microclimate.--Nest site selection is of importance to insure development and emergence of hatchlings. Apparently females make no effort regarding post-natal qualities (resources, competition, and predation) of the nest site. Hatchling survivorship was significantly lower at the Main Gate area, where most nest sites were observed at Tucson in this study.

In the Tucson population all nest sites were observed at the base of stone walls; the majority (74%) being located in the soil base of the north or east face of a stone wall. At Agua Caliente one nest site was observed at the base of a 25 cm diameter horizontal branch of a Celtis reticulata (netleaf hackberry) that was partially embedded in the soil. The location of nests with a particular directional exposure or in association with objects in contact with the ground suggests avoidance of areas exposed to excessive incident solar radiation and evaporation; such positions reduce dessication and exposure to extreme

heat. Partially excavated nests are often left abandoned. While the cues for exact site selection or avoidance for egg deposition remain unquantified they appear to involve both soil moisture and temperature.

Of four nests, depth varied from 60 to 130 mm and the angle from 30 to 45 degrees below horizontal. The 60 mm nest had reached rock bottom but the female deposited her eggs anyway. A nest tunnel is filled up to 2/3 leaving an air filled chamber above. The clutch of eggs is usually deposited 10 to 45 mm from the bottom, perhaps to avoid submersion.

A diurnal temperature cycle is provided in Table 12 for two nest sites; one on the north side of a stone wall and the other on an east side. The nests were within 10 meters of each other and recorded on August 3 and 4, 1979. The data indicate the importance of a few hours of direct exposure to sun for both the maximum temperature and total range. The north side nest varied in deep-nest temperature from 31.3 to 32.0 °C and the east side nest varied from 33.3 to 37.5 °C. The north facing nest site was monitored for seven days with a mean \pm 2SE of 33.2 ± 1.1 °C and range of 31.7 to 35.4 °C. These temperatures were recorded between 1500 and 1822 hrs in August 1979.

Nest Site Competition.--Females alternate digging with frequent stops, rest stops and look-out stops for rival females or predators. The average duration of a rest stop was 1.33 minutes and that of digging was 3.72 min for a female observed for 1.5 hours. Interestingly, this female alternated digging between two sites, changing three times during this period.

Table 12. Hourly temperature profiles for Tucson nest sites with northern and eastern exposures for August 3 and 4, 1979. All temperatures in degrees celcius at 2 m above ground, 5 mm above ground, ground, and below ground nest chamber.

Time	Northern Exposure				Eastern Exposure			
	2m	5mm	Ground	Nest	2m	5mm	Ground	Nest
1700	36.5	33.8	27.4	31.9	36.9	35.4	34.0	36.8
1800	35.8	32.2	27.7	31.9	35.8	34.6	34.0	36.5
1900	34.6	31.4	26.7	31.9	34.8	33.9	33.7	36.2
2000	33.4	29.0	28.1	31.9	33.7	32.2	32.1	36.1
2100	29.6	28.8	27.2	31.9	33.0	30.7	31.2	35.7
2200	27.8	28.6	26.8	32.0	27.8	30.1	30.8	35.4
2300	26.9	26.9	26.5	32.0	27.0	28.0	29.3	35.1
2400	26.1	26.2	26.8	31.9	26.0	27.9	28.8	34.9
0100	25.9	26.1	26.0	31.8	25.9	27.4	28.9	34.6
0200	23.6	23.7	25.3	31.8	23.6	24.1	26.6	34.3
0300	21.5	24.2	25.6	31.6	21.2	23.5	25.7	34.1
0400	22.1	24.0	25.8	31.4	21.9	24.2	27.5	33.7
0500	24.1	23.7	25.4	31.3	23.3	23.5	24.9	33.3
1200	33.4	32.5	32.0	31.4	34.5	41.6	46.8	36.8
1300	34.7	32.2	30.9	31.6	35.5	40.8	44.4	37.5
1400	35.4	33.1	29.6	31.7	35.9	36.2	37.4	37.5
1500	35.8	33.1	29.8	31.7	36.7	36.3	36.0	37.0
1600	34.3	30.9	29.4	31.7	34.3	33.6	33.7	36.6

Nest digging was observed as late as 2000 hrs in July. The first excavation of a nest site takes two days to complete. Other females are able to utilize the same site and complete the job in only one day. One nest site, on the north side mentioned above, was known to be used by four females in six days.

Nest sites are only defended while the females are digging. A female will respond to another's approach with push-ups and/or a chase. Nest competition could be unusually high at the Tucson population because of the scarceness of adequately situated nesting soil and the coralling effect of the stone walls, but this may also occur in linear riparian habitats. The fact that at least nests are defended suggests some evolutionary response to competition. The isolated observation of a female excavating two nests simultaneously is strongly suggestive of competition.

Egg Mortality.--Of nine nest excavations that were observed to completion, previously laid eggs were dug out and left on the surface in three cases involving a total of seven eggs. Other observations of egg mortality include eggs that were torn, collapsed, or lost to fly larvae when buried in the soil. In the last case, it is likely that some freshly laid eggs are parasitized by flies just prior to the nest being filled in. Of four nests that were reopened, a total of 14 out of 38 (36.8%) eggs were "bad." These estimates of egg mortality could be low. Blair (1960) reports 75-78% for Sceloporus olivaceus due primarily to nest predation by Salvadora, the diurnal patch-nosed snake. There are no snake species on the Tucson campus study area.

Egg and Hatchling Size

Eggs recently laid generally measure 10 X 6 mm with a mean weight of 0.24 g. Those recovered 20 days old measure 12.5 X 10 mm and weigh 0.66 g. The parchment shelled eggs of this species are ectohydric, absorbing water from the soil. The strategy is important to desert lizards in offsetting the loss of a scarce resource to reproduction when it is available in the form of soil moisture (Tracy and Snell 1985). It may also allow females to carry more eggs when predator evasion clutch volume are mutually constraining.

At Tucson, data on eggs hatched in the laboratory and from hatchlings with soil on their heads collected above nest sites, reveal an August mean SVL of 20.1 ± 0.1 mm and range of 18 to 22 mm for 46 lizards. Of 20 male hatchlings the mean is 20.1 ± 0.2 mm, range 18 to 22 mm; 15 females average 19.9 ± 0.2 mm and range 18 to 21 mm. There is a drop in the proportion of small hatchlings as the season progresses suggesting a possible increase in hatchling size.

Relative Clutch Mass and Clutch Size

Mean relative clutch mass is 38.3% of total (37 - 41%, N = 3), determined from the masses of females and eggs immediately after oviposition. Clutch size (CS) at Tucson ranged from 6 to 15 with a mean \pm 2SE of 9.6 ± 1.3 for 15 clutches sampled. At Agua Caliente, 15 clutches range from 4 to 12 with a mean \pm 2SE of 7.3 ± 1.2 . Interpopulation differences in mean adult female SVL is the simplest explanation for the difference in mean CS observed.

July clutch data are plotted and regressed on SVL in Fig. 12 for both populations combined. The results demonstrate a good linear

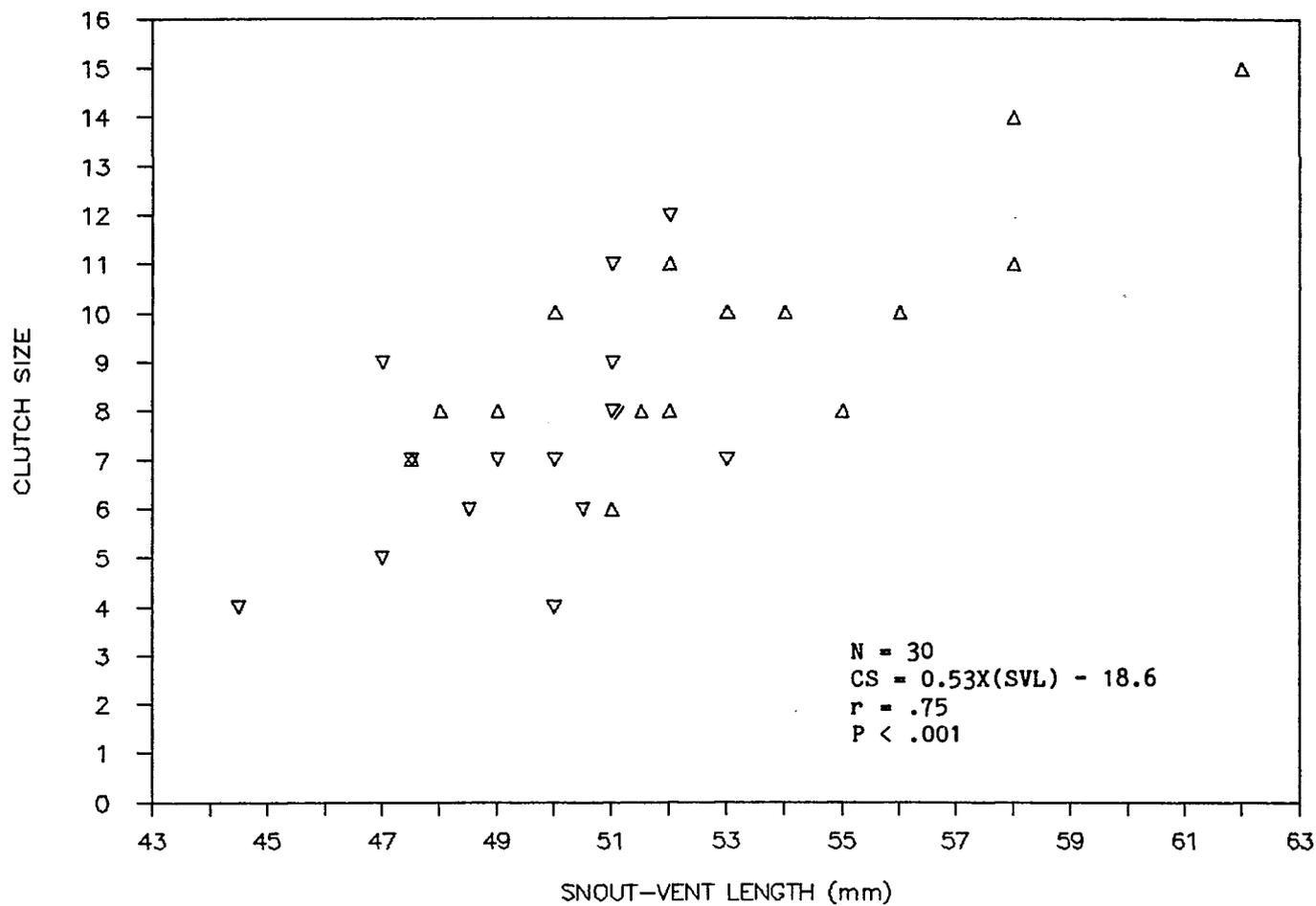


Fig. 12. Clutch size plotted on female snout-vent length of Urosaurus ornatus, in July. Up-triangles (△) for Tucson and down-triangles (▽) for Agua Caliente; regression equation provided for all points.

relationship between CS and SVL ($r = 0.75$, $P < .001$). Two females undergoing tail regeneration produced smaller than expected clutches. Clutch size and SVL for the two are 7/53 and 8/55; the residuals are -2.5 and -2.6 ova respectively. Five August clutches range from 6 to 11 with a mean of 8.0 for both populations combined.

There is not sufficient recapture data on late hatching females to determine if they have lower fecundity than earlier hatching females. Smaller clutch size is expected on the basis of smaller SVL. One female (#304) first captured on February 26, 1980 at 29.5 mm SVL appears to be of a later clutch. It was subsequently recaptured in gravid condition on both July 1 and August 12 of 1980, indicating that some late hatching females are capable of producing two clutches in their first year of adulthood.

Patterns of Variation in Reproductive Effort

In the present study clutch size varied from 4 to 15. Michel (1976) reports up to 16 eggs per clutch for the species. Atypically small mean clutches reported for U. ornatus are: 4.8 by Parker (1973) for a xeric site at South Mountain, Maricopa Co., Arizona; 4.0 by Douglas (1966) for Mesa Verde National Park in Colorado; and 3.5 by Gehlbach (1965) for the Zuni Mountains in Northern New Mexico. The last two may represent genetic geographic variation. Clutch size (CS) for the species ranges 2 - 16 eggs per clutch. CS was reported by Dunham (1982) to vary between populations, independently of female SVL.

Some of the patterns of reproduction reported are as follows. Clutch size generally increases with female SVL but the correlation (r) is near zero for late clutches (Martin 1977). Dry years, presumably

through resource limitation, yield both smaller eggs and clutches (Ballinger 1977). Clutch size decreases as the reproductive season progresses; hatchling size (and probably egg size) tends to increase.

The late season clutches of Urosaurus ornatus and other lizards are generally smaller and may yield larger hatchlings. Females can reduce clutch size and egg size for a considerable period of time after the initial establishment of CS, but can only increase egg size and not CS if extra resources become available subsequently. Martin (1977) reports an increase in the frequency of follicular atresia in August females of U. ornatus in Texas. The net effect is an inequality imposed by physiological limits on the ability to adaptively regulate reproductive effort.

Theoretically, clutch size should decrease with increasing resource unpredictability (later in the season) from bet hedging suggested by Nussbaum (1981). Alternatively, resources may be predictably less available in the late season, or females are investing more per egg if fewer but larger late hatchlings would enhance fitness (Smith and Fretwell 1974, Ferguson and Bohlen 1978, and Ferguson and Snell 1986). If offspring of later clutches experience higher mortality, then it will be maladaptive for a female to produce a large second clutch when it does little to improve current effective fecundity but has a negative impact on residual reproductive value.

Movement

The distribution of tree lizards within the habitat indicates changes resulting from the dispersal of hatchlings, nest site location by females, seasonal shifts in basking sites, and emigration. The

overall movement is presented in Table 13. The highly sedentary nature of this species is readily indicated by the majority of recaptures occurring at the same site. Another obvious feature is the second mode at 20-30 m travelled by females at Tucson for which all eleven points are represented by gravid or post-partum females moving to or from nesting sites.

The majority of nest sites at Tucson were observed in the Main Gate area where the spring sex ratio was 16 males to 15 females in contrast with 9 males to 41 females in the summer nesting season for all years combined. These observations indicate that many females locate nest sites outside of their daily home ranges.

Dispersal and Site Selection by Juveniles

Shortly after hatching, neonates select elevated perches near ground level that allow them to bask and scan for prey items. These perch sites are often fallen branches, stones, roots, or low on the trunks of trees and shrubs. Larger juveniles in the fall are more equally distributed and more elevated on shrubs, trees, and stone walls at Tucson. At Agua Caliente, juveniles are commonly observed on dead desert broom, saplings, trees, larger fallen branches and occasionally cholla. This pattern along with recapture data indicates a steady dispersal away from the nest sites.

Juveniles probably move steadily along and stop when subjected to the right cues. Smaller juveniles may be restricted by larger juveniles to the lesser structures in the fall and spring seasons. Lizards of various sizes are often observed at a single site at one time, in the fall and early spring and peer chasing is common.

Table 13. Movement of Urosaurus ornatus at Tucson and Agua Caliente indicating number of individuals recaptured per distance interval.

Distance Traveled (m)	Tucson				Agua Caliente			
	Males		Females		Males		Females	
	Juv	Adult	Juv	Adult	Juv	Adult	Juv	Adult
0	41	74	43	66	8	18	13	18
0 < 5	13	29	12	17	1	1	4	1
5 < 10	3	12	5	9	0	2	0	0
10 < 15	3	7	3	3	1	0	0	0
15 < 20	3	1	3	5	1	2	2	0
20 < 30	2	1	2	11	1	0	0	0
30 < 40	1	1	0	2	0	1	0	1
40 < 50	0	1	1	1				
50 < 100	1	1	1	3				
100 < 150	1	1	0	1				
150 +	0	1	0	0				

Juveniles appear to defend small feeding territories; some of these sites clearly did not offer refuge from predators. Finally, the pattern of adult home ranges may result just as much from differential mortality, among sites varying in quality, as from actual site selection.

Winter Aggregations

During the cooler months, October through March, lizards tend to congregate at sites providing shelter against freezing. Some of these sites may provide opportunity for basking and activity on warmer sunny days, perhaps giving some lizards the advantage of an extended growing season. On cool mornings tree lizards have been found under fallen bark at Agua Caliente. An earlier study at Agua Caliente in 1959 - 1961 found many lizards in hibernacula in dead limbs and trunks of mesquites in late November-December (Lowe and Tremor unpubl).

Emigration and Annual Site Fidelity

A comparison, between populations, of the proportion of recaptures involving movement reveals $161/385$ (41.8%) at Tucson and $18/75$ (24.0%) at Agua Caliente (Table 13); differing significantly ($\chi^2 = 7.65$, $P < .01$). Movement is defined as travel between sites (trees or sections of stone walls). Actual emigration rates are relatively low in this study. If all movement over 50 m is considered as emigration, then it accounts for 2.5 percent of all recaptures at Tucson. There are some "floaters," small males that appear unable to establish a territory or home range in the saturated Tucson campus population. Two examples are #97 and #331. Male 97 was recaptured at three different stations,

moving at least 108 m, and last measured 51.0 mm SVL at one year of age. Male 331 was recaptured at four different stations, moving a minimum of 52 m, and last measured 50.5 mm SVL at ca. 18 months of age. The mean SVL for adult males is 55.8 ± 0.3 mm.

The majority remain on a single tree or stone wall most of the time and occasionally travel to adjacent sites. Only approximately 25 percent of all recaptures involve lizards taken at different stations within 10 m. Individuals with multiple recapture data confirm that most captures occur at one station and a few at one or two adjacent sites. Home range size depends on the proximity of elevated perch sites but is also influenced by interaction with conspecifics and other species.

Life-history

The reproductive cycle of this species clearly anticipates a summer rainfall period to provide optimal conditions for incubation and hatchling growth. This pattern contrasts with that of Uta stansburiana, another small iguanid widespread throughout the west, which responds more to winter precipitation (Asplund and Lowe 1964). The geographic range and presumably the origin of the genus Urosaurus is centered in Mexico where summer precipitation predominates. Urosaurus graciosus is a more western desert representative of the genus and is exposed to a productivity regime which is mostly determined by winter precipitation. This species also has a reproductive cycle timed to summer rainfall (Vitt and Ohmart 1975). Winter productivity is predominantly terrestrial where temperatures are higher. Uta is a terrestrial genus and Urosaurus is semi-arboreal, suggesting a relationship between habit, microclimate, and life cycle among genera.

Life Tables

Life tables for Urosaurus ornatus appear in Tables 14 and 15 for males and females at Tucson. Data used to generate survivorship are in Tables 7, 8, and 9. Adult SVLs at ages in interger years were interpolated from Fig. 9; July clutch size was similarly interpolated for females from Fig. 12, while the mean August CS is 8.0. The Tucson population appears able to sustain itself with a net replacement rate (R_0) of 1.32. It is unlikely that the calculated value of $R_0 = 1.32$ is significantly different from 1.0. The estimate of egg mortality is probably conservative.

A little more than half of the egg production in the population is from females two or more years old. This may be unusual for U. ornatus, however not for many Sceloporus species. On the other hand, some populations of Uta stansburiana are capable of a complete annual turnover of individuals. Given the reproductive potential in Urosaurus ornatus and its early maturity, it too should be capable of complete annual turnover. This is obscured when adult mortality is the independent demographic variable to which juvenile mortality is inversely dependent.

The life table of U. ornatus (Table 15) is remarkably similar to that of the much larger spiny lizard (Sceloporus clarki) provided by Tinkle and Dunham (1986). The key difference is the greater generation time of S. clarki; 25% mature in one year and 75% mature in two years. It produces a single clutch per season. Survival to maturity, annual adult survival, and fecundity are nearly identical for the two taxa, as well as the types of environments they occupy in nature. The population

Table 14. Life table for Urosaurus ornatus males at Tucson.
 q_x = age specific mortality rate, l_x = proportion surviving
 from egg to age X, e_x = life expectancy at age X.

Age = X years	SVL _x mm	q_x	l_x	e_x
0 Egg		0.419	1.000	0.439
0.1 Hatchling		0.601	0.581	0.584
0.3 Juvenile		0.674	0.232	0.961
0.8 Subadult		0.368	0.0756	1.414
1 Adult	53.7	0.391	0.0478	1.920
2	56.5	0.572	0.0291	1.512
3	59.3	0.800	0.0124	1.201
4	62.1	1.000	0.00249	1.000

Table 15. Life and fertility table for Urosaurus ornatus females at Tucson.
 q_x = age specific mortality rate, l_x = proportion surviving from egg to age X, m_x = fecundity at age X, v_x = reproductive value at age X, e_x = life expectancy at age X. Replacement rate (R_0) = 1.32.

Age = X years	SVL _x mm	q_x	l_x	m_x	$l_x m_x$	v_x	e_x
0 Egg		0.419	1.000				0.512
0.1 Hatchling		0.571	0.581				0.708
0.3 Juvenile		0.643	0.249				1.185
0.8 Subadult		0.143	0.0889				1.917
1.0 Adult	50.4	0.400	0.0762	4.0	0.305	17.280	2.093
1.1			0.0732	4.0	0.293	13.502	2.038
2.0	52.3	0.530	0.0457	4.5	0.206	15.736	1.822
2.1			0.0433	4.0	0.173	11.859	1.768
3.0	54.2	0.500	0.0215	5.0	0.108	15.832	1.748
3.1			0.0204	4.0	0.082	11.411	1.688
4.0	56.1	0.500	0.0107	5.5	0.059	14.117	1.502
4.1			0.0102	4.0	0.041	9.053	1.426
5.0	58.0	1.000	0.00537	6.0	0.032	9.600	1.000
5.1			0.00483	4.0	0.019	4.000	0.900

density of the semi-arboreal S. clarki is much lower and individuals cannot utilize smaller shelters available to Urosaurus ornatus. In the Lower Colorado Desert, where S. clarki is absent, it is replaced by S. magister which is more terrestrial and is able to utilize ground rodent nests throughout the year. In this xeric habitat the semi-arboreal Urosaurus is able to find thermal buffering and refuge from predators beneath bark, in wood cracks, and in other elevated sites generally too small for adults of larger-bodied species.

Population Regulation

Some age and sex classes may often exceed their carrying capacities that are temporally and locally variable. Available evidence for density-dependent mortality in this species includes egg mortality from nest competition (Tucson population), increased hatchling survivorship following experimental density reduction (Ballinger 1976), and high mortality of males from territorial behavior (sex ratio). Vertebrate predators of U. ornatus also likely respond, both numerically and functionally to variations in prey density whether seasonal or annual.

Population density control in a widespread species such as Urosaurus ornatus occurs through interaction with an environment that is both variable and unpredictable. Multiple clutching is characteristic of small-bodied, early maturing, opportunistic species. Urosaurus ornatus and many other iguanid lizards evidently produce more offspring than are necessary to compensate for adult and juvenile mortality. Less fit offspring are subjected to higher mortality rates by "overflowing" into less preferred habitat and by attracting more predators. High

reproductivity provides a buffer against occasional unpredictable high mortality.

Iguanid lizards tend to produce larger clutches than lizards of other families (Stearns 1984). In the western hemisphere, iguanid lizards often predominate in deserts, on beaches, riverbanks, and in other harsh or disturbance situations. Interestingly, in the fossil record they do not diversify until the Eocene, paralleling the appearance of non-equitable climate.

Much of the basic r- K- pattern centers on the correlation between body size and associated life-history traits. Given age of maturity alone, earlier maturing (generally smaller) forms will outreproduce all others. The allometric advantage of small size can be augmented or overridden at any point by the combined effects of other selective forces. Urosaurus ornatus is a small bodied species. Small size is as important to the ability to mature in a single season as it is to success as a semi-arboreal Anolis-like life-form.

The resolution of reproductive tactics into two strategies by Tinkle et al (1970) is based on an allometric pattern. An obligate overwinter period, in temperate regions, restricts the age of first reproduction to one, or more than one, season following hatching. Small-bodied species that mature in one year form a distinct temporal mode from the later maturing large-bodied taxa. Widespread species often vary--presumably adaptively--in size and age at maturity, and in clutch size and frequency (Fitch 1970, 1980). Even within populations,

a proportion of individuals may mature in one season with the remainder reaching maturity in the next.

Dunham (1982) attempted to correlate resource supply/demand ratios with life-history variables at four different U. ornatus populations. The results of ranking the populations according to density, survival, and reproductive effort were not consistent with the predictions of r- K-selection theory. This test of r-K-theory fails because the populations are evolutionarily similar and ecologically different. The current data base may not be able to resolve genetic components of life-history variation on an interpopulation level.

Unless one knows that the observed differences between populations stem from evolved as well as extrinsic factors, then perhaps it should not be attributed to r- or K-selection in the same sense (Balliger 1976). It appears that a population should be able to respond (in sex ratio, age and size structure) in a short time to changes in the demographic and physical environment, exhibiting a shift in life history traits without evolution. In r- K-theory, the Tucson population of U. ornatus is best considered an r-species in a current K-environment. Increased food resource productivity and decreased predator pressure are implicated with increased population density and increased intraspecific competitive pressure in producing an urban insular effect in ecological time in the Tucson population studied.

Summary of Part II

Density of Urosaurus ornatus in the Tucson population averaged 99 per hectare for 1979 and 1980, twice that of Agua Caliente with 48 lizards per hectare in 1979. Movement of lizards within the study areas

is also nearly double at Tucson, involving 42% of all recaptures compared to 24% at Agua Caliente. Movement over 50 m occurred in 10 (2.5%) of Tucson recaptures; and none over 40 m occurred at Agua Caliente.

Maximum longevity is at least 5 years at Tucson and at least 3 years at Agua Caliente. Survivorship from egg to adult is 4.8% for males and 7.6% for females at Tucson. Hatchling survival was significantly lower in the heavily used Main Gate area. Survival was lower for later hatching or second clutch offspring. Annual survivorship of year old adults is greater than those two or more years old. Average annual adult survivorship at Tucson is 49% compared to 33% at Agua Caliente. Known causes of mortality are predation, freezing, and egg failure. Egg mortality from adult female nest site competition was observed at Tucson.

Gravid females were observed in June, July, and August. At least some late hatching females produce two clutches of eggs in their first year. Average July clutch size was 9.6 at Tucson and 7.3 at Agua Caliente. Clutch size increases linearly with female SVL; the range was 4 to 15 for females 44.5 and 62.0 mm SVL respectively. The net replacement rate (R_0) at Tucson was determined at 1.32 with 55% of the productivity contributed by females two or more years old.

RESULTS AND DISCUSSION

PART III. BEHAVIOR

Large scale activities in the life-history, such as growth, reproduction, and their timing, are treatable as physiological properties--adaptations--of an organism. There are many behavioral elements by which the lizard responds, relatively quickly, to less predictable situations. Although lizards exhibit many kinds of distinctive behavior, only a few were investigated in this study. The relevance of thermoregulation, foraging, and social behavior to the life-history of Urosaurus ornatus is explored within the context of the annual activity cycle of the species in southern Arizona.

Annual Surface Activity Cycle

At Tucson, tree lizards are active on campus in every month of the year. At Agua Caliente, no individuals were captured in December, January, and February. Relative surface activity of males and females, illustrated in Fig. 13 for all captures, varies significantly between seasons. Males greatly outnumber females in March whereas females greatly outnumber males in July, August, and September. Captures of young-of-the-year (YOY) show males outnumbering females. Smaller YOY females enter into winter dormancy later in the fall and emerge earlier in the spring than do male or larger female YOY lizards (see Figs. 6 and 7). Smaller adults of both sexes appear to remain active later in the fall than larger adults (see Part I--Seasonal Patterns).

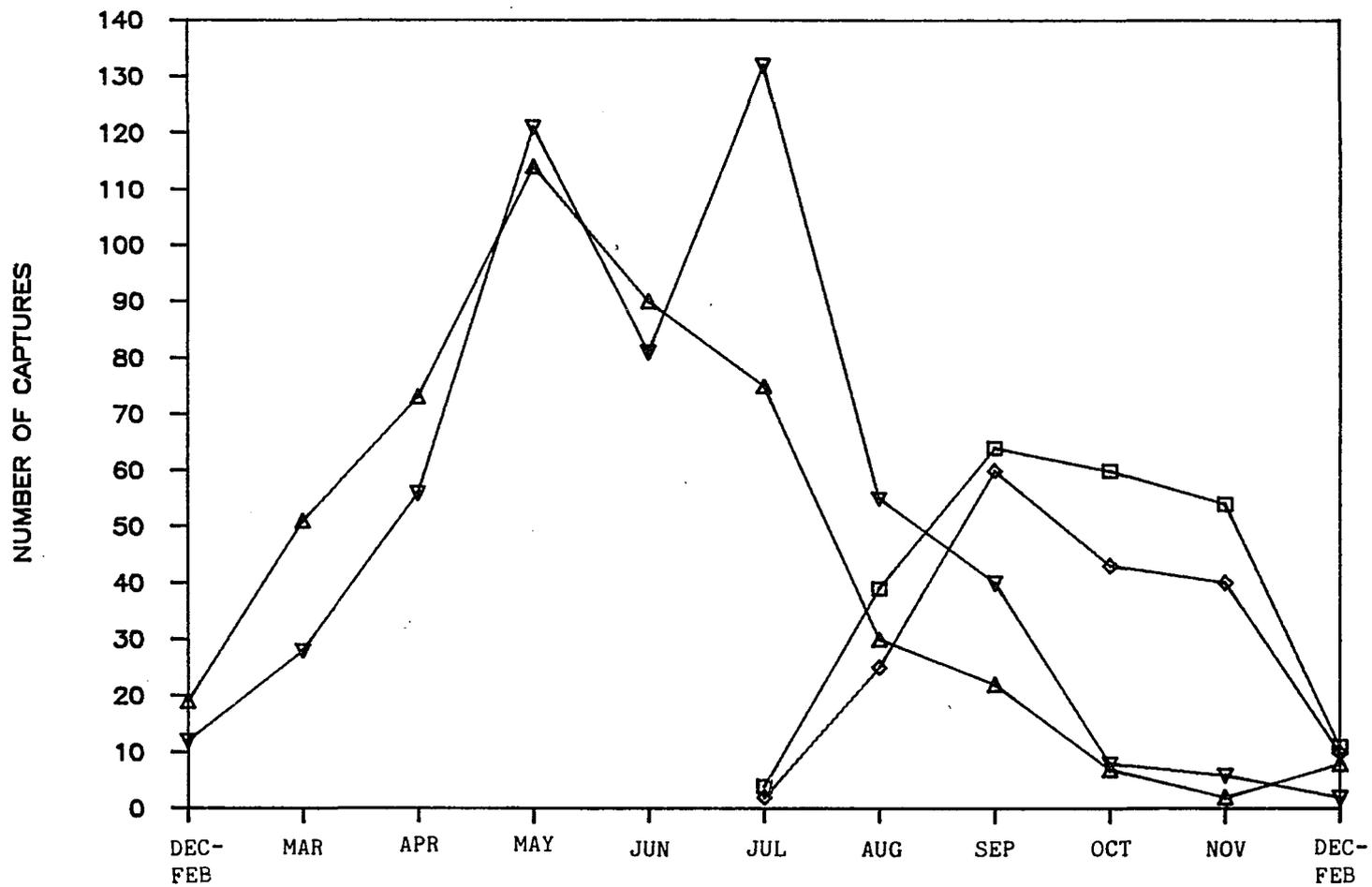


Fig. 13. Total captures of *Urosaurus ornatus* in this study, indicating relative surface activity of adult males up-triangles (▲), adult females down-triangles (▼), young males squares (□), and young females diamonds (◇).

The sex ratio of individuals registered once per period was determined to vary from unity in hatchlings to 1.55 (females over males) in adults. The pattered described above suggests differences in relative surface activity between subgroups of the population. I find that as a group females are less surface active than males except in the reproductive season. As a consequence of reduced foraging opportunities, females reach adult size later than do males. On the other hand, smaller individuals, male or female, may be more surface active than their peers in order to "catch up" in SVL or stored energy.

Thermoregulatory Behavior

Preferred and critical temperatures are among the intrinsic factors differing between U. ornatus, U. graciosus, and species of Sceloporus that are ecologically similar to Urosaurus. The temperature gradient in the habitat is one parameter that is correlated with microhabitat partitioning among coexisting sceloporine lizards (Gates 1963; Barnes 1974; and Vitt, van Loben Sels, and Ohmart 1981). U. ornatus has a broader thermal activity range than U. graciosus associated with its broader seasonal activity period (Gates 1963).

The thermal profile of U. ornatus outlined in Table 16 indicates an activity range of approximately 20 to 40 °C for deep body temperatures observed in this study. Successful thermoregulation will maintain a temperature closer to 37 °C (preferred body temperature). The amount of activity as well as the proportion spent on thermoregulation is, of course, dependent on environmental temperatures.

Mean daily minimum temperatures are lower at Agua Caliente year round; mean daily maxima are lower January through May. Minimum

Table 16. Deep-body thermal profile for Urosaurus ornatus.

	46.98 °C	30 °C acclimated	Tremor	1962
	46.86	35 "	Tremor	1962
Critical	46.39	30 "	Gates	1963
Thermal	46.39	25 "	Tremor	1962
Maximum	45.31	15 "	Tremor	1962
	44.5	30 "	Lowe and Vance	1955
	43.1	Field Controls	Lowe and Vance	1955
Maximum	41.2	July	Gates	1962
Voluntary	40.1	July	This Study	
	39.5	May	Vance	1953
Mean	38.33	Sept.	Gates	1963
or	38.18	July	Gates	1963
Eccritic	36.91	April	Gates	1963
or	36.81	April-May	This Study	
Preferred	36.8	May	Vance	1953
	34.5	Sept.-Oct.	Vance	1953
Minimum	20.2	April	This Study	
Voluntary	19.7	March	Lowe and Tremor	Unpubl.
Critical				
Thermal	---			
Minimum				
Supercooling				
Limit	-5.56	Lowe, Lardner, and Halpern		1971

environmental temperatures ($^{\circ}\text{C}$) for an active lizard in this study are: 20.2 deep body directly after emergence, 22.2 stone surface, 20.2 air inside crevice, 20.9 at 5 mm air outside, and 20.7 at 1.5 m air. There were no lizards observed at air temperatures less than 20°C , yet many were observed with temperatures just above 20°C . The threshold for initial surface activity appears to be 19 to 20°C (66 to 68°F). More time available to forage at the Tucson population should provide for greater individual growth and reproductive productivity, assuming resources are available.

Foraging Behavior

Tree lizards are predominantly sit-and-wait predators approaching and capturing insects that are sighted at a short distance. They often perch low on the trunks of trees and will travel to over 3 meters to capture an insect on or close to the ground. Sometimes a lizard will stop and perch on a small stone or fallen twig after taking an insect on the ground, otherwise they are strictly semi-arboreal or saxicolous except when nesting.

The most frequently captured prey observed in this study include Hymenoptera (mostly Formicidae), Lepidoptera (including larvae), and a mixture of small Coleoptera, Diptera, and Homoptera. A lizard will frequently go farther to capture a larger prey item. Small insects are also "picked off" while lizards, generally males, patrol their territories. More information on diet and foraging is provided by Asplund (1964), Barnes (1974), Dunham (1980, 1983), and Vitt et al (1981). On several occasions a male was seen stealing a large insect

from the mouth of a female after which the male displayed with push-ups. This probably happens to smaller individuals of either sex.

Social Behavior

Many populations of iguanid lizards are of sufficient density to lead to frequent intraspecific interactions. This is especially true for Urosaurus ornatus. Characteristically on one of its numerous elevated perch sites, an individual can communicate visually both within and across home range boundaries.

Displaying

Both males and females of this species exhibit an assertive display. This has been frequently observed in the field when lizards move from one location to another, immediately after devouring prey, or when approached by an intruder.

The species-specific pattern was described for captive animals by Carpenter and Grubitz III (1960); I have added here information from direct field observations in local natural habitats. The pattern consists of a series of push-ups beginning with two, each held for more than one second and separated by a pause, followed by one to four more that are not separated by pauses, but the first (third in the sequence) is held for a moment. The push-ups involve all four limbs or, sometimes, just the hind limbs. Very small juveniles were frequently observed doing push-ups in the summer and autumn seasons, perhaps with reference to a feeding territory or a refuge from predators.

While most information on display behavior is derived from observing males, females are known to exhibit many of the same behaviors.

Only males possess ventral patches of blue or a blue gular region. When engaged in push-ups, tree lizards will arch their backs, slightly flattening the body laterally to expose ventral patches of blue. They also extend a dewlap and raise the tail. These details are much more exaggerated in escalated interactions between two males, or a male and a female.

In this study all emerging lizards were very dark in dorsal coloration, as usual at the commencement of basking during morning hours. Later, throughout the day, males generally remained noticeably darker than females regardless of substratum, sun, shade, or temperature. Dominant males were not always darker in color than subordinate males of approximately the same size as reported for captive males in artificial environments. According to Carpenter and Grubitz III (1960) dominant males are much darker or nearly black in dorsal coloration when compared to subordinates. They report that coloration changes quickly and when a dominant lizard is removed from an enclosure containing several males, the next individual in the dominance hierarchy will become very dark and assume the dominant position. In captivity as in natural environments, dominant males initiate more social interactions, including courtship, than other males.

In the natural habitat, escalated conflicts between individuals in the field may lead to a rarely observed, although undoubtedly common, lateral face-off. This appears to be in a clockwise fashion, exposing each other's right side. Natural toe-loss data indicate a greater loss on the right side (56:36, $Z = 11.68$, $P < .01$), apparently a result of biting during face-off behavior. The conflicts between males generally

end with a chase and/or biting. Many individuals loose toes, tails, and occasionally a limb. Scars are frequently noted on the lower jaw, and, to a lesser extent, the upper head region of adult males. The lateral face-off has never been observed between two females although they do display at, and chase, one another.

Milstead (1970) found display behavior between male U. ornatus to be less complex and resulting in more fighting than that of Sceloporus merriami. He attributed this to U. ornatus being more "primitive." It is more likely that these two species in different genera have simply followed different strategies for different reasons.

Courtship Observations

Courtship behavior has been observed both in the field and in an indoor enclosure. At Tucson, in the spring, dominant males have been observed performing the characteristic push-up sequence within a few centimeters of (subadult) females. Often the female will respond by completing the sequence in synchrony with the male, occasionally she does not respond, and rarely does she run off. Larger females are rarely observed at this time. These events occur prior to the mating season, and may serve to condition females for reproduction and/or establish mating advantages by familiarity.

Observational notes on mating behavior appear below for a case in the field and one in the artificial enclosure.

July 2, 1979 at Tucson (Field)

- male gives push-ups, female replys. Male gives more, then bobs head rapidly and climbs on top, then bites at neck and twists left side under. Female not too receptive - ran off after two seconds.

July 5, 1979 at Tucson (Enclosure)

- 0930 clockwise movement (face-off), the male bites into female's tail from right, 5-10 mm down. Push-ups by both. Then (male) crawls on top, bites into neck area, and inserts left side under.
- 0936 still biting in neck, but not inserted.
- 0937 she runs off, he bites at and hits left flank, hanging on. Both under log now.
- 0940 push-ups by both now, lifting of male's tail.
- 0941 "rapid head bobbing by male, then tail is elevated and accompanied by push-ups".
- 0943 let loose of her, more rapid head bobbing.
- 0945 got her by the neck skin.
- 0948 still got her by the neck.
- 0952 she runs off, he doesn't chase. Both do push-ups after.
- 0953 lots of rapid head bobbing and push-ups, new female on log giving push-ups back. More bobbing and push-ups - female does push-ups and is coming down off log.
- 0955 another female, responding - rapid head bobbing by male with dewlap out and lateral compression.
- 0956 another female - he's looking up - she's looking down, push-ups by both and rapid head bobbing (male).
- 0957 female gives gape - more push-ups by male.
- 0958 (male) bites at female running by. Dewlap, push-ups, head bobbing.
- 1000 bit female at tail again, on right side, giving push-ups while hanging on.
- 1001 inserts left side under for one second.
- 1008 male and female move into clockwise face-off, give each other push-ups.
- 1010 male removed.

Note: Females compress their trunks, showing no blue.
Females do give push-ups but don't bob.

Male Reproductive Success

Male reproductive success in U. ornatus appears to depend on the ability to establish a territory adjacent to, overlapping, or encompassing female home ranges. Variation in male reproductive success is known to be widespread but it is not easily linked to genetic changes in a population. Sexual selection can, nevertheless, be reasonably inferred from extant features related to male rivalry (intrasexual selection) or mate preference (intersexual selection). Male rivalry is widespread in

iguanids but there is little if any observational evidence of female choice in pair formation.

Male reproductive success is affected by three classes of activities: 1) gaining access to females, 2) preventing other males from accessing females, and 3) mate preference. As a group, iguanid lizards are sedentary and rely primarily on visual communication for social and many other activities.

Individuals of many lizard species remain in or return to the same home ranges year after year. While it would be more expected in longer lived species that may become more familiar with the habitat, it is clearly evident in Urosaurus ornatus as well. Younger individuals may be selecting sites based on the presence of some older adults.

Home range selection by females will ultimately affect the reproductive success of the males in a population. Males may have no role in this selection, as in Sceloporus jarrovi (Ruby 1981) where females are first to leave winter aggregation sites and establish home ranges. Males of some temperate species, including Anolis carolinensis (Greenberg and Noble 1946) and Urosaurus ornatus, emerge from winter inactivity sooner than do females and establish territories.

It is not known how males affect home range selection by females. The presence of heterospecific males may repel females (Hunsaker 1962 Sceloporus torquatus group, and Gates 1963 Urosaurus graciosus); they would tend to end up on sites defended by a conspecific male. Females may seek sites defended by a conspecific male, even when other species are absent. Adult female U. ornatus have been observed on trees with Sceloporus clarki at Agua Caliente and other sites. They

have frequently been observed at stations without conspecific males. At Saguaro National Monument (east of Tucson), female U. ornatus (already gravid) remained in their home ranges after experimental removal of males, even through the second mating period (M`Closkey, Baia, and Russell 1987a). Conversely, males increased movement and eventually abandoned territories following experimental removal of females; departure time decreased as the proportion of females removed increased (M`Closkey, Baia, and Russell 1987a, 1987b).

Territorial behavior.--Observations of habitat use by Urosaurus ornatus indicate two distinct patterns on the study areas. On sites where suitable habitat is distributed in a regular disjunctive fashion, as trees in a woodland, there is generally one adult male and one or two females per tree. The tree centers a territory that is actively defended by the adult male against intrusion by other adult males. Males are often seen patrolling their territories, displaying as they move from one perch to another or making a complete loop back to a preferred shelter and/or perch. In May, adult males were observed dragging their femoral-pore region across the tree surface at various points in the territory. Undoubtedly some of this behavior is regulated by the visual awareness and activity of other lizards in the area.

In a different situation, suitable habitat may be distributed continuously, as at rock out-crops, and many adult males will utilize the same area. In this habitat type there will be only one lizard on a perch at a time but it may be forced out by another more dominant individual. Here the picture is one of shifting dominance for a single

perch site, not a whole territory containing multiple advantageous perch sites.

Dominance hierarchies appeared to form where winter aggregations occur, when the males emerged in the spring. At Agua Caliente none were observed in the summer with more than two males per station. Presumably dominants enjoy more uninterrupted matings and frequently interfere in the courtship attempts of subdominant males. Subordinate males, or those in peripheral areas, can gain access to females by waiting for a resident dominant male to be lost or weakened, and then take over the territory; it may otherwise "steal" mating opportunities if they arise.

Additional observations in the spring reveal that larger dominant males tolerate juveniles. The juveniles don't flee when approached by the dominant, but other adult males do flee and tend to stay just outside of the dominant's visual field or at least, at an unpursued distance. The dominant will chase the other adult males, usually after a display of raising the tail and waving it over the body, arching with all four limbs extended, lateral flattening, dewlapping, and rapid push-ups. In a dominance hierarchy it may be advantageous for the smallest lizards to locate themselves as close as possible to a dominant lizard to minimize interference by individuals of intermediate status. A direct observation in the field made in this study supports this prediction, and invites further study.

Throat Color Variation

Colors, used for visual communication are an interesting feature of iguanid lizards. Both Urosaurus ornatus and U. graciosus are special in that they exhibit sexual dimorphism and individual variation in the

bright colors of the gular region. Gates (1963) hypothesized that the demographic environment may affect the development of gular color in male U. graciosus.

Neonate U. ornatus are virtually without any display colors. Small juveniles of both sexes have orange throats. Adult females retain this orange color, although sometimes it is pale or yellowish. In contrast, as males differentiate and mature they exhibit gular colors progressing from orange to yellow to green and finally to turquoise blue. More than one color may be present, even in old adults, with the bluest color towards the center and reddest on the outside, sometimes forming concentric rings.

Of all adult males at Agua Caliente, 56.3 percent acquire turquoise in their gular colors compared to 37.3 percent at Tucson. This difference is significant ($X^2 = 6.45$, $P < .05$) and it may indicate an effect on development correlated with a greater availability of territories at Agua Caliente.

Adult males rarely regress in gular coloration, i.e. lose the bluest colors. Some exceptions appear to be seasonal, whereas others may be due to loss of social status. In 1979 and 1980 two adult males on the Anthropology Wall (Fig. 2), a high density region, emigrated to other stations and their gular colors changed from green to yellow.

Interestingly in this same region, males with turquoise throats predominated in 1979 - 1980. There was no male recruitment for two years. From 1981 on, these individuals gradually disappeared and were replaced by younger males. This later replacement group was predominantly of males with orange and yellow throats. Throat color

variation should be investigated further at the Tucson population and at other populations of the species.

Summary of Part III.

Tree lizards are active in every month at Tucson; none were observed to be surface active in December, January, or February at Agua Caliente. The extended activity of the Tucson population is attributed to higher environmental temperatures in the winter. The threshold for activity is a minimum ambient temperature of 19 to 20 °C.

Despite a sex ratio favoring females, captures of males greatly exceed those of females in March. Males begin to exhibit territorial behavior at this time. Captures of young-of-the-year were also greater for males than for females. Smaller YOY females and smaller adults of both sexes appear to remain surface active later in the fall season than do larger individuals.

Tree lizards are predominantly sit-and-wait predators that frequently shift from one perch site to another. Adult males are most conspicuous; they vigorously defend territories against intruding adult males. Males generally possess scars on the head and tend to lose toes on the right side of the body, indicating a species or population specific preference for a clockwise face-off during conflicts. At the less dense Agua Caliente population, 56.3% of the males develop blue in their gular colors compared to 37.3% at the Tucson population. Gular color may indicate social status of individuals and the availability of territories in the population.

CONCLUSIONS

When life-histories are examined using reproductive value as a measure of fitness, one can often relate observations to one or more explanations. Many life-history traits are subject to adaptive compromise. Of these, the tradeoff between productivity and survival appears to have resulted in different life-histories for male and female U. ornatus.

Given maximum net reproductive rate as the basis of selection on females and the seasonality imposed by the local environment, it is possible to explain their observed annual activity pattern. Females are less surface active than males in the prereproductive period, and are most active in the reproductive and post-reproductive periods (late summer). Females are especially secretive in the spring, thereby better avoiding predation; the small minimum size of maturity reduces the need for greater surface activity related to foraging. Any female that survives will reproduce.

Male fitness is best measured by the number of successful matings; therefore, a premium is placed on territorial defense and greater body size. Survival does not guarantee reproductive success. The activity pattern is characterized by greater surface activity of juvenile males than juvenile females in the fall and spring, spring territorial activity in adult males, and relatively less activity in the post-reproductive period. In spite of differing modes of energy expenditure on reproduction in males (competition) and in females (egg

production), it is likely that relative surface activity (foraging intensity) is the proximate cause for most of the difference in body size between sexes. Sexual selection (territoriality) and predator avoidance are the principle selective factors on males and females respectively.

What ultimately limits the body size of tree lizards is not clear. The advantages of early maturity are obvious. It is also evident that growth and longevity are relatively limited in the natural population at Agua Caliente compared to the human-altered environment of the urban Tucson population. Growth rates may naturally decrease with age. Survivorship and reproductive productivity increase with body size; at some point it is likely that survivorship begins to decline with size, as larger individuals become more vulnerable to and favored by predators.

Differences in demographic parameters between the two study populations of U. ornatus are not inconsistent with the common predictions of r-K-selection theory. Greater body size, longevity, population density, and reproductive productivity of the urban Tucson population are expected of an r-species thrust into a K-environment. The significant demographic differences between the two populations of Urosaurus ornatus studied, do not require evolutionary explanations; they can be explained by developmental and ecological factors in ecological time.

APPENDIX A

NONLINEAR REGRESSION--PROGRAMMING AND MODELS

DEC-10 programming for nonlinear regression analysis.

File 1. SYST.CDC
.PETER,BN6430402L.
PW,----.
FTN5.
BMD83AR,B.

File 2. BMDPAR.FOR
SUBROUTINE FUN(F,P,X,N,KASE,NVAR,NPAR,IPASS,XLOSS)
DIMENSION P(NPAR),X(NVAR)
F=P(1)-(P(1)-X(1))*EXP(P(2)*X(2))
C F=(P(1)*X(1))/(X(1)+(P(1)-X(1))*EXP(P(2)*X(2)))
C F=((P(1)**3*X(1)**3)/(X(1)**3+(P(1)**3-X(1)**3)*
C 1 EXP(P(2)*X(2))))**(1/3)
RETURN
END

File 3. FILE1.BMD
/PROBLEM TITLE IS 'ASYMPTOTIC GROWTH'.
/INPUT VARIABLES ARE 3.
FORMAT IS '(6X,F3.0,2X,F4.1,2X,F4.1)'.
/VARIABLE NAMES ARE TIME,SVL1,SVL2.
/REGRESS DEPENDENT IS SVL2.
PARAMETERS ARE 2.
/PARAMETER INITIAL ARE 57.0.-.01.
NAME=A,r.
/END

To execute program, set up for the von Bertalanffy model as shown,
using male growth interval data:

.TOCDC SYST.CDC,BMDPAR.FOR,FILE1.BMD/NOEOR,MALE.DAT

Notation for growth equations:

L, L_1, L_2 = SVL, initial SVL, recapture SVL

L_0 = SVL at hatching (age = 0) A = asymptotic SVL

D = time elapsed between captures (days) t = age in days

r = characteristic growth rate

von Bertalanffy model:

Growth rate = $dL/dt = Ar[1 - (L/A)]$

SVL = $L = A(1 - be^{-rt})$ $b = (1 - L_0/A)$

Interval equation: $L_2 = A - (A - L_1)e^{-rD}$

Logistic-by-length model:

Growth rate = $dL/dt = Lr[1 - (L/A)]$

SVL = $L = A/(1 + be^{-rt})$ $b = (A/L_0) - 1$

Interval equation: $L_2 = AL_1/[L_1 + (A - L_1)e^{-rD}]$

Logistic-by-weight model:

Growth rate = $dL/dt = (rL/3)[1 - (L^3/A^3)]$

SVL = $L = [A^3/(1 + be^{-rt})]^{1/3}$ $b = (A^3/L_0) - 1$

Interval equation: $L_2 = \left[\frac{A^3 L_1^3}{L_1^3 + (A^3 - L_1^3)e^{-rD}} \right]^{1/3}$

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