

A POPULATION MODEL OF THE LIZARD *UTA STANSBURIANA* IN SOUTHERN NEVADA¹

FREDERICK B. TURNER, PHILIP A. MEDICA, KENT W. BRIDGES,² AND
ROBERT I. JENNRICH³

Laboratory of Biomedical and Environmental Sciences, University of California,
Los Angeles, California 90024 USA

Abstract. Population densities, reproduction, and survival of the lizard *Uta stansburiana* were measured at the Nevada Test Site in southern Nevada, USA, between 1964 and 1974. These data were used to develop a model of the population dynamics of this species. Results of irrigation experiments in 0.4-ha enclosures near Mercury, Nevada, were used to formulate multiple-regression equations predicting frequency and size of clutches laid by two age-classes of females in terms of winter rainfall, March air temperatures, and *Uta* population density. Densities of *Uta* in these enclosures were manipulated, and age-specific survival modeled in terms of spring densities of *Uta*. Experiments in which an important predator on *Uta* (the leopard lizard, *Crotaphytus wislizeni*) was removed from enclosures were used to estimate the influence of the predator on basic survival rates of hatchling and older *Uta*. The model was generally developed from data acquired in the small enclosures, but predictions were compared with actual observations of changes in *Uta* populations in Rock Valley (19 km west of Mercury, Nevada) between 1966 and 1972.

Agreement between model predictions and actual numbers was fair. The model predicted a decrease in density from 1966 to 1967, but numbers of *Uta* actually increased conspicuously at this time. This was the only major discrepancy between predictions and observations. The observed mean spring density (\bar{d}) between 1967 and 1972 was 41.4 *Uta*/ha (SD = 20.8), while the model predicted a mean density of 37.8 *Uta*/ha (SD = 13.6). Observed and predicted mean proportions of yearlings in spring populations were identical (0.78).

The basic version of the model estimated different survival rates for two age-groups of adult *Uta*. A simpler version of the model, using a common survival rate for both age-groups, gave predictions essentially identical with those of the basic model. Other tests of the basic model showed it to be most sensitive to changes in winter rainfall and predation pressure, much less so to air temperatures. Fifteen- and 30-yr synthetic sequences of predator densities were used to examine model stability over longer periods of time. When predator densities were drawn randomly from distributions with a mean of 2 individuals/ha, model populations exhibited lower mean numbers and amplitudes than actually observed during 9 yr in Rock Valley.

The basic model included three density-dependent parameters: clutch frequency, clutch size, and adult survival. The model was modified so that (1) egg production was density independent, while adult survival was not; (2) adult survival was density independent, but egg production was not; and (3) there was no density dependence in the model. Thirty-year tests showed that cases 1 and 2 did not differ markedly from the basic model, although the removal of one density-dependent constraint resulted in slightly higher mean densities. In case 3, the model lacked stability and predicted numbers increased to unrealistic levels within 5 yr. We conclude that processes relating to egg production were modeled more effectively than those influencing survival, and that improvement of the model will depend on more detailed studies of the impact of predation on age-specific survival rates of *Uta*.

Key words: desert; field experiments; lizard; model; population dynamics; southern Nevada; *Uta stansburiana*.

INTRODUCTION

Between 1964 and 1973 effects of low levels of gamma radiation on vertebrate populations were studied in four 9-ha areas in Rock Valley, Nevada (latitude 36°43'N, longitude 116°11'W). Rock Valley is 19 km west of Mercury, Nevada, at the United States Department of Energy's Nevada Test Site (Fig. 1). In addition to studies of radiation effects, research in

Rock Valley has provided information on natural fluctuations in size and composition of rodent and saurian populations (Turner et al. 1969a, b, c, 1970, Medica et al. 1973, French et al. 1974).

We became interested in the hypothesized influence of winter rainfall on lizard reproduction (Mayhew 1966a, b, Zweifel and Lowe 1966) and adduced supporting evidence for this effect on populations of the small iguanid *Uta stansburiana* (Hoddenbach and Turner 1968, Turner et al. 1970). Later field experiments involving irrigation, density manipulations, and predator removal were carried out with *Uta* occupying 0.4-ha enclosures 1.6 km west of Mercury between 1969 and 1973 (Turner et al. 1973, 1974).

The dynamics of populations of *Uta stansburiana*

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² Present address: Department of Botany, University of Hawaii, Honolulu, Hawaii 96822 USA.

³ Present address: Department of Mathematics, University of California, Los Angeles, California 90024 USA.

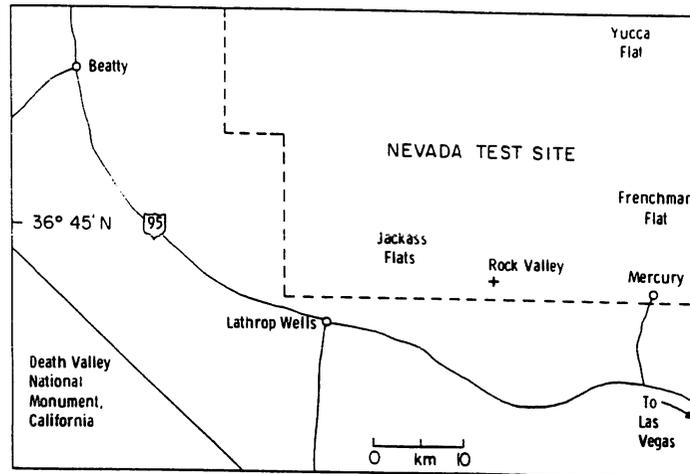


FIG. 1. Area map of Rock Valley and adjoining portions of Nye County, Nevada, and Inyo County, California.

(Tinkle 1967) and of other lizards have been extensively studied in this country (see review by Turner 1977), and many potential factors influencing numbers have been explored. However, no model capable of integrating such effects and predicting the numerical response of a lizard population has been devised. We believe there is heuristic value in developing such models. Furthermore, a model predicated on realistic input variables and incorporating actually observed or experimentally derived processes may be used to explore theoretical questions of regulation and stability of numbers (Reddingius 1971). We have attempted this task, drawing on 10 yr of experience with populations of *Uta stansburiana*.

As pointed out by Watt (1962), the deductions which may be drawn from models are only as valid as the assumptions used to construct them. Therefore, we made no a priori assumptions as to how the model should work, but based its operation on what we observed in the field and on the results of field experiments designed to yield quantitative measures of relevant ecological processes. No density dependence was built into the model unless data indicated the presence of a mechanism which could act in this manner. Naturally, we could not model all possible processes impinging on numbers of *Uta*, and some of the model parameters (e.g., mortality rates) represent net interactions of several factors. However, given the nature of our data base, work carried out in one location over a period of 10 yr, we believe that we have achieved a high degree of biological reality in our model.

A problem commonly encountered with models of this nature is validation. One usually develops models with all the information at hand and there is then no convenient way to test the work independently. This point was brought out in the panel discussion of an analysis of regulation of numbers of Great Tits by Dhondt (1971:547). We were able to base almost all of

our model on observations and field experiments carried out in the 0.4-ha plots near Mercury and test it against estimated population trends in Rock Valley.

REPRODUCTION BY *UTA* IN SOUTHERN NEVADA

General background

Uta stansburiana breeds during the spring and females lay from one to seven clutches of eggs, depending on body size and environmental conditions (Medica and Turner 1976). The first clutch of eggs is laid in April (rarely late March), after which subsequent clutches are laid at intervals of 1 or 2 wk. Egg laying may extend into early July. The first clutches of the season are usually the largest, and clutch size typically declines during the remainder of the breeding season. As a group, 2nd-yr and older females always lay more clutches than yearling females. In the ensuing text we discuss different age-groups of lizards, usually distinguishing between yearling and older individuals in spring populations. If eggs are laid between mid-April and the end of June, lizards hatching from these eggs and surviving until March are from 8–10½ mo old (age is calculated from the time the egg is laid; 2nd-yr lizards are from 20–22½ mo old, etc. For convenience we will refer to these age-groups as “yearlings” and “older lizards,” or “9-mo-old lizards” and “20+-mo-old lizards.”

The dominant environmental influence on egg production by *Uta* is winter rainfall (Turner et al. 1974, Medica and Turner 1976). It is known that in years with high winter rainfall, growth and production of winter annuals is enhanced. It has further been postulated, both for *Uta* (Hoddenbach and Turner 1968) and for other Mohave Desert lizards (Mayhew 1966a, b, Zweifel and Lowe 1966), that increased biomass of annual plants leads to more insect food. Strong indirect evidence in support of this view was given by

Turner et al. (1973). More direct comparisons were made by Sanborn (1977), who analyzed the abundance and varieties of food in stomachs of *Uta stansburiana* collected in Rock Valley in 1971, 1972, and 1973. These findings were compared with D-Vac[®] and pit-fall-sampling data taken during the same years. Insect-sampling data showed that many kinds of arthropods were more abundant in seasons following low winter rainfall, while numbers of other species decreased under such conditions. However, the amount of food in *Uta* stomachs in 1973 was about 22% greater than in 1971. *Uta* ate more in 1973 as a result of overall increased abundance of insects and/or because individual prey items were larger. Dunham (1980) showed that foraging success and growth rates of *Sceloporus merriami* and *Urosaurus ornatus* in Texas were greater in years of higher rainfall.

No experimental evidence of a temperature effect on *Uta* egg production has been derived from field observations or experiments, but laboratory experiments with other lizards have shown that air temperatures have an important controlling effect on timing of vitellogenesis and the deposition of the first egg clutch in the spring (Licht 1972). Temperature may also play a role in the timing of subsequent clutches.

Egg production is also influenced by body size of breeding females, a characteristic of most oviparous lizards (Fitch 1970:207). As a group, older female *Uta* (≥ 20 mo) produce larger clutches than do yearling females (Hoddenbach and Turner 1968, Medica and Turner 1976). Density may be another intrinsic factor that affects egg production because body size of *Uta* appears to be inversely correlated with spring density (Turner 1977:200).

If this is true, it follows that egg production (per individual) will be lower in dense populations and higher in sparse ones. The 1972 field experiments did not show a density effect on clutch size over the range of densities examined (30–90 *Uta*/ha). Further experiments in 1973 indicated a density effect on clutch size of older females, but not on that of yearling females. These experiments involved initial densities ranging from 15–133 *Uta*/ha (Turner et al. 1974).

Winter rainfall and egg production

The hypothesis that reproduction by some Mohave Desert lizards is positively correlated with winter rainfall rests on several causal links, viz., that (1) increased rainfall leads to increased net production by annual plants, (2) the enhanced growth of annuals fosters greater productivity by arthropods feeding on them, and (3) the increased arthropod biomass provides more food for *Uta* and promotes greater egg production. Some of these ideas were tested by field experiments in small enclosures 1.6 km west of Mercury.

Five 0.4-ha fenced plots were used in 1969–1970. Between 28 October and 3 December 1969, 50 mm of

water were applied by sprinkler to one of the plots. Time between applications averaged ≈ 3 d. The soil of this plot was kept moist until irrigation was completed. Five enclosures were also used in 1971–1972. Between 8 and 21 November 1971, 50 mm of water were applied to two of the plots. Natural winter rainfall (September–March) was 58.5 mm in 1969–1970 (24.4 mm during October–November and 31.1 mm during February–March) and 41.1 mm in 1971–1972 (39.9 mm during December).

During May 1970 and late March 1972, winter annuals were counted in irrigated plots and adjoining nonirrigated plots. All winter annuals in quadrats were collected and dried, and their mass was determined. Fieldwork with lizards began in mid-February in 1970 and 1972. *Uta* were captured by noosing, and conventional records of identity, sex, location, length, mass, and sexual condition were maintained. During the breeding season nearly every female was captured at least once a week. Clutch sizes were inferred from palpation and counts of follicles ≥ 5 mm in size. Yolke follicles are hard when palpated and can be rolled between the fingers like BBs. With a little experience the number can be well estimated. Hoddenbach and Turner (1968) showed that follicular atresia occurs only occasionally among yearling females and not at all among older individuals. Numbers of clutches laid were estimated from body mass changes and palpation data (Turner et al. 1970).

Additional water applied during November of 1969 and 1971 had obvious effects on germination and growth of winter annuals during ensuing growing seasons. In 1970, combined dry masses of annuals in the irrigated plot were ≈ 8 g/m², in the control plot 0.5 g/m². In 1972 the mean dry mass of annuals in two irrigated plots was ≈ 5 g/m²; mean standing crop in two control plots was ≈ 0.1 g/m². Plot-specific data for various kinds of plants were given by Turner et al. (1973: Table 2).

Analyses of body mass changes among *Uta* ≥ 8 months of age between March and July showed that, except for ovigerous females, masses of lizards ≥ 20 mo old were fairly stable. Body mass data pertaining to 22 yearling females in the spring of 1970 were summarized by Turner et al. (1973: Table 3). The difference in mean mass changes among *Uta* in watered (830 mg) and unwatered plots (506 mg) was significant ($t_{20} = 2.29$, $P = .036$).

A similar approach was followed with the 1972 data but the analysis included both males and females (Table 1). A 2×2 factorial analysis of variance indicated highly significant effects due to irrigation and sex, but no significant interaction. F values for treatment and sex were 18.6 and 24.4 respectively, with $F_{.01} = 7.3$. The difference between males and females was apparently associated with egg production and the diversion of energy by females into eggs rather than into new somatic tissue. In both sexes there was apparently

TABLE 1. Changes in mass observed in 1972 among yearling *Uta stansburiana* in 0.4-ha enclosures in southern Nevada.

Sex	Treatment	n	Mean initial mass (g) (\pm SE)	Mean change in mass (g) (\pm SE)
Male	Watered	6	2.71 \pm 0.24	0.82 \pm 0.22
	Unwatered	16	2.90 \pm 0.09	0.22 \pm 0.10
Female	Watered	8	2.23 \pm 0.14	0.14 \pm 0.13
	Unwatered	14	2.54 \pm 0.06	-0.33 \pm 0.08

more energy available in irrigated plots, whether for reproduction or growth, and this energy could only have come from more available food. These findings give strong direct support for the previously assumed relationship between abundance of annual plants and food available for ground-dwelling insectivorous lizards. Dunham's (1980) investigations of relative prey abundance in dry (1975, 1977) and wet (1976) years in Texas showed that both *Sceloporus merriami* and *Urosaurus ornatus* had more prey available during the wet year.

Population density and egg production

Body size and density.—Turner et al. (1965) discussed growth and body size of *Uta stansburiana* in four 9-ha areas in Rock Valley. In 1964–1965 hatchling *Uta* in Plot 2 were significantly smaller than those in the other three plots. Plot 2 also supported a higher density of *Uta* than any of the other three areas. These authors suggested that if body size differences were density dependent, then over a period of years the highest density of *Uta* might occur in one of the other areas, with a consequent reordering of interplot differences in body sizes.

Between 1966 and 1972 all four areas exhibited increases and declines in numbers of *Uta*. However, except in 1969, Plot 2 regularly sustained the highest density of *Uta*. During this time mean spring body masses of *Uta* also changed from year to year. We analyzed relationships between densities and body masses in four sex- and age-groups of *Uta* (yearling males and females, older males and females), but will discuss our findings only in terms of yearling females. Mean spring body masses of yearling females and densities in four areas are given in the Appendix. An analysis of covariance was made of these masses and densities. This analysis showed a highly significant inverse relationship between body masses and densities ($t = -4.35$, $P = .000$). Analyses of yearling males and lizards 20+ mo of age showed similarly statistically significant relationships. Here, and in subsequently described covariance and regression analyses, data were examined to detect gross departures from assumptions of additivity, homogeneity of slope and variance, and normality on which reported t and F tests were based. There was no compelling evidence

of nonhomogeneity of variance. Residual analyses showed, in some instances, outliers and other departures from normality, but we were reluctant to delete the former, and the latter were not judged of sufficient magnitude to justify transformations.

The foregoing analysis showed that average body masses of *Uta* in dense spring populations are depressed relative to long-term average expectations, while lizards that comprise sparse spring populations are relatively heavier. The correlation between body mass and density may or may not be indicative of a causal association between the two. If there is a cause and effect relationship, the simplest interpretation would involve some form of intraspecific competition. If food were present in limited quantity, growth could be retarded at high densities simply because of smaller rations per individual. Both adult male and female *Uta* are territorial (Tinkle 1967), and increased social interaction at higher densities might also be postulated as affecting body mass, even in the presence of unlimited food resources.

Although Tinkle (1967: 49) did not observe body size differences during his study of *Uta stansburiana* in Texas, inverse correlations between body size and density have been noted among mammals (Scheffer 1955), fish (Nikolsky 1963:149–150, Carlander 1969:17), snails (Foin and Stiven 1970), pupae of blowflies (Webber 1955), spruce budworms (Morris 1963), and larvae of pine loopers (Klomp and Gruys 1965, Klomp 1966). In fact, Watt (1971:572) has suggested this relationship as a "core" principle of environmental science.

Body size and clutch size.—How does clutch size among females of the same age (size) vary with body mass, aside from other sources of variation? This question was examined by covariance analyses of clutch size, based on either (1) the number of eggs present in both oviducts or, if there were no oviductal eggs, (2) the number of corpora lutea in the ovaries. Counts of yolked follicles were not used because of possible follicular atresia among younger females (Hoddenbach and Turner 1968). The body masses of females with oviductal eggs were reduced by masses of the eggs themselves.

The covariance analyses involved clutch size (C), 16 time categories (i.e., four months in each of four years; t), and body size (B) of female *Uta*. The model analyzed was of the form:

$$C = \alpha_t + \beta B + e. \quad (1)$$

Preliminary analyses had shown that the 16 slope values did not differ significantly. Clutch sizes were analyzed for the months March, April, May, and June for the years 1965–1968 inclusive. Two analyses were made: the first with body mass as the covariate, the second with snout-vent length as the covariate (Table 2). In all four covariance analyses the slope (β) was positive, indicating a direct correlation between body

TABLE 2. Covariance analysis of clutch size (C) and body size (B , measured two ways) in two age-groups of *Uta stansburiana* from southern Nevada ($C = \alpha + \beta B$). Net mass is the gross body mass minus the mass of oviductal eggs and oviducts.

Age	n	Covariate B	Probability of true slope = 0	df	$\beta \pm SE$
Young	135	Net mass	0.072	168	0.345 ± 0.192
Old	247	Net mass	0.031	230	0.322 ± 0.149
Young	185	Body length	0.000	168	0.147 ± 0.041
Old	247	Body length	0.000	230	0.148 ± 0.034

size and clutch size. Tests of the null hypothesis $\beta = 0$ gave borderline P values when body size was expressed as net mass, and clearly significant probabilities when expressed as snout-vent length. Clutch size, then, varies among years and months because of external influences (e.g., temperature, rainfall), but is also affected by population density and body size.

Numbers of clutches

The number of clutches laid during the reproductive season is the single most important variable influencing numbers of eggs produced by *Uta* in the Mohave Desert (Turner et al. 1970, Medica and Turner 1976, Turner 1977). It is unfortunate that there is no easy way to determine the number of clutches laid by unrestrained lizards. We devoted considerable effort to this objective between 1966 and 1973, both in Rock Valley and the Mercury plots (Turner et al. 1974, Medica and Turner 1976, Turner 1977). Table 3 summarizes information pertaining to numbers of clutches among *Uta* in the two locales. This table pertains only to females that survived the entire reproductive season. Females that died during the spring laid fewer clutches. Table 3 does not include data from plots ar-

TABLE 3. Mean numbers of clutches (\pm one standard error) laid by *Uta stansburiana* in southern Nevada.

Year	Locale	Yearlings		Older	
		n	No. clutches $\pm SE$	n	No. clutches $\pm SE$
1966	Rock Valley	9	4.00 ± 0.24	5	4.60 ± 0.40
1967	Rock Valley	16	1.94 ± 0.14	9	2.33 ± 0.24
1968	Rock Valley	13	3.31 ± 0.17	8	3.75 ± 0.16
1969	Rock Valley	14	3.29 ± 0.27	4	4.25 ± 0.25
1969	Mercury Valley	13	2.77 ± 0.26	4	4.25 ± 0.25
1970	Mercury Valley	32	0.94 ± 0.12	8	1.75 ± 0.16
1971	Rock Valley	15	2.93 ± 0.15	3	3.67 ± 0.33
1972	Rock Valley	23	2.87 ± 0.18	4	4.00 ± 0
1972	Mercury Valley	17	2.71 ± 0.21	6	2.83 ± 0.17
1973	Rock Valley	22	5.73 ± 0.12	8	6.00 ± 0.38
1973	Mercury Valley	34	4.59 ± 0.14	15	5.13 ± 0.19
Means			3.19		3.87

TABLE 4. Mean numbers of clutches (\pm one standard error) laid by older female *Uta stansburiana* in 0.4-ha enclosures in southern Nevada.

Year	Plot	Experimental manipulation	March density (n/ha)	Number of older females	Mean no. clutches
1969	6	None	67.5	2	4.00 ± 0
	7	None	70.0	2	4.50 ± 0.50
1970	6	Irrigated	95.0	2	3.00 ± 0
	7	None	82.5	4	1.75 ± 0.25
	8	None	75.0	1	1.00
	9	None	52.5	1	2.00
1972	10	None	50.0	2	2.00 ± 0
	6	Irrigated	50.0	2	4.00 ± 0
	7	Low density	30.0	1	3.00
	9	High density	85.0	3	2.67 ± 0.33
	10	High density	90.0	2	3.00 ± 0
1973	13	Irrigated, high density	77.5	2	4.00 ± 0
	7	Low density	17.5	1	6.00
	8	Low density	17.5	2	6.00 ± 0
	9	High density	110.0	4	5.00 ± 0.41
	10	High density	132.5	5	5.00 ± 0.32
	13	Intermediate density	45.0	1	4.00

tificially irrigated before the breeding seasons of 1970 and 1972. The table also reflects minor corrections in 1972 and 1973 data from the Mercury plots (see Turner et al. 1974).

Yearling females clearly lay, on average, fewer clutches than older females. Females ≥ 20 mo of age will often lay one clutch early in the spring before any 9-mo-old females reproduce. When mean numbers of clutches of yearling females (F_y) were regressed on those of older females (F_o), a highly significant ($r^2 = .90$) linear relationship was obtained:

$$F_y = 0.98F_o - 0.63. \quad (2)$$

Hence, when older females lay from 2 to 5 clutches, the expected number of clutches laid by younger females is ≈ 0.7 less.

Earlier in this section we identified several possible extrinsic factors (winter rainfall and temperature) and two intrinsic factors (density and body mass) which might influence egg production. We now examine numbers of clutches laid by females in terms of these variables. Our approach to this problem can be enhanced by considering the 1970-1973 data from Mercury Valley in terms of individual plots (in Table 3 we combined data from all nonirrigated plots and gave overall means). Table 4 summarizes plot-specific data from Mercury Valley and includes March densities taken from Turner et al. (1974: Tables 1 and 10).

The data in Table 4 were analyzed by stepwise multiple linear regression using three combinations of winter rainfall measured near the plots (September-March rainfall, October-March rainfall, and November-January rainfall), average December air temperature and

average March air temperature (both measured in Rock Valley), and *Uta* density in the enclosures as six independent variables. The first three variables entered (giving an R^2 of .90) were September–March rainfall, March air temperature, and *Uta* density. The R^2 value associated with September–March rainfall was .71, and rainfall and air temperature together accounted for 88% of the observed variation. F values for entry of rainfall and temperature were highly significant ($F = 37$ and 19 , respectively), but that for density ($F = 2.6$) was statistically nonsignificant. We included the density term in the equation because of the relationships among density, body size, and egg production already set forth. The equation predicting number of clutches laid by older females in terms of these variables is:

$$F_a = 0.029R + 0.165T - 0.0066d - 1.22, \quad (3)$$

with R = total rainfall (millimetres) between September and March, inclusive, T = average March air temperature (degrees Celsius), and d = spring density of *Uta* (number per hectare).

Clutch size

Hoddenbach and Turner (1968) and Medica and Turner (1976) presented 10 yr of clutch size data for *Uta stansburiana* in Rock Valley. Averages were computed for the months of April, May, and June for yearling and older females. Clutch size was influenced by age, month, and year (Hoddenbach and Turner 1968). Medica and Turner (1976) attempted to generalize these data and derive relationships between average clutch sizes of old and young females in different months. Our approach will be to estimate mean size of April clutches of older females in terms of winter rainfall, temperature, and population density, and predict other clutch sizes in terms of the April estimate.

April clutch size among older females.—Sizes of the first (or first and second) clutches laid in the Mercury plots in 1970 (five plots), 1972 (six plots), and 1973 (five plots) were summarized by Turner et al. (1973, 1974). Plot means ranged from 3.50 to 5.00 in 1970, from 4.14 to 5.00 in 1972, and from 4.60 to 5.50 in 1973. Irrigated plots were included, and winter rainfall for 1969–1970 and 1971–1972 was increased 50 mm because of artificial watering. Clutch size estimates for plots were analyzed in terms of the same independent variables used in the analysis of numbers of clutches laid. September–March rainfall, average March air temperature, and *Uta* density entered in the same order as in the analysis of numbers of clutches. The R^2 value for rainfall was .54, and rainfall and air temperature together accounted for 64% of the observed variation. Density brought the total R^2 to .70. The equation predicting April clutch size C_A from these data is:

$$C_A = 0.0097R + 0.046T - 0.0046d + 3.34. \quad (4)$$

April clutch sizes of older females and later clutches.—When sizes of early (April) and later (May, June,

July) clutches are compared, early clutches are almost invariably larger. The only significant exception to this occurred in 1965, when clutches were larger at the end of the season than at the beginning. Hoddenbach and Turner (1968) discussed this phenomenon and attributed it to the unusual spring rains in 1965, when 72 mm of rain fell during March (12 mm) and April (60 mm). This particular pattern of rainfall was not duplicated in any other year between 1964 and 1973, and the 1965 data were not used in comparisons of April, May, and June clutch sizes. When May clutch sizes (C_M) were regressed on April clutch sizes for 9 yr between 1964 and 1973, the following relationship was obtained ($r^2 = .55$):

$$C_M = 0.94C_A - 0.37. \quad (5)$$

When June clutch sizes (C_J) were regressed on April clutch sizes for 9 yr the relationship was as follows ($r^2 = .51$):

$$C_J = 0.64C_A + 0.15. \quad (6)$$

Medica and Turner (1976) reported that only 55 lizards collected between 1965 and 1973 contributed to estimates of July clutch sizes, and concluded that an estimate of 2.6 for all July clutches (for both yearling and older females) was a satisfactory approximation.

Clutch sizes of yearling and older females.—When average clutch sizes of yearling females in Rock Valley for the months of April, May, and June (1964–1973) were regressed on corresponding average clutch sizes of older females the following relationship was obtained ($r^2 = .74$):

$$C_Y = 0.66C_O + 0.72. \quad (7)$$

Thus, yearling clutch sizes range from ≈ 80 to 90% of adult clutches of three to five eggs. The data on which this analysis is based were given by Hoddenbach and Turner (1968) and Medica and Turner (1976).

For the foregoing, it is possible to estimate mean monthly clutch sizes of females of both age-groups, given an estimate of the size of the April clutch among older females C_A . The May clutch size of older females (C_M) is estimated by Eq. 5, June clutch size (C_J) by Eq. 6, and April, May, and June clutch sizes of yearling females (C_A , C_M , and C_J) are estimated by Eq. 7, using appropriate values of C_A , C_M , and C_J . This system has merit in its simplicity, but has the disadvantage of accumulating errors, particularly in estimating mean clutch sizes of younger females.

The biological points to be derived from the foregoing are as follows. First, during the 10-yr period between 1964 and 1973, mean clutch sizes of older females during April (based on March and April samples), May, and June always exceeded mean clutch sizes of yearling females in these months. Second, in every year except 1965 the trend in both age-groups was from larger clutches early in the season to smaller ones in June. Third, reproduction during July is limited and may not occur in some years.

SURVIVAL OF *UTA* IN SOUTHERN NEVADA*Survival of hatchlings*

Survival of hatchling *Uta* was evaluated between 1969 and 1973 in 0.4-ha enclosures in Mercury Valley. Juvenile lizards were marked during the summer, and survival of individuals evaluated by censuses the following spring. Only lizards marked between 1 July and 31 August at snout-vent lengths ≤ 28 mm were considered in our analyses of hatchling survival. Hence, our starting rosters of marked lizards did not include those animals which had already survived one of the more vulnerable periods of their lives. Minimal survival estimates were based on numbers of marked lizards recovered the ensuing spring. We examined data from two plots in 1969–1970, four plots in 1970–1971 and 1971–1972, and six plots in 1972–1973. These data were given by Turner et al. (1973: Table 15, 1974: Table 8). Overall mean survival was 44% for males, 58% for females. Survival of male and female hatchlings was compared by χ^2 tests for each of 4 yr. Although joint survival of both sexes ranged from as low as 33% (1969–1970) to as high as 68% (1971–1972), χ^2 totals based on comparisons of male and female survival were insignificant ($\chi^2 = 0.2$ to 1.9, 1 df). This agrees with an earlier analysis of age compositions and sex ratios of unrestrained *Uta* populations in Rock Valley (Turner et al. 1969a) and with what Tinkle (1967) observed in Texas. We adopt, then, an overall hatchling survival rate of 51% in 0.4-ha enclosures.

Is survival of hatchling *Uta* correlated with numbers of young lizards hatched during the summer? This is not easy to assess directly because at no time did we determine the absolute abundance of hatchling lizards. Turner et al. (1974:123) regressed 9-mo minimum survival of hatchling *Uta* in six plots (1972–1973) on estimated total egg production, assuming the latter to be a reasonable approximation of total numbers of young. This analysis failed to show a significant correlation between egg production (or numbers of young) and 9-mo survival.

The 9-mo survival rates of hatchlings observed in enclosures were generally much higher than those observed in Rock Valley. Turner et al. (1970) reported 9-mo survival of hatchling *Uta* in Rock Valley to be 24% in 1966–1967 and 19% in 1967–1968. Turner (1975: 120) gave 16% for 1966–1967, 19% for 1967–1968, 26% for 1968–1969, 19% for 1969–1970, and 31% for 1970–1971. The value for 1966–1967 (16%) was in error, and should have been 24% (the earlier reported value).

The 0.4-ha plots in Mercury Valley were fenced, and there was no opportunity for emigration by marked hatchlings. The study plots in the 9-ha fenced areas in Rock Valley were so small (1.44 ha) relative to the size of the enclosures that the resident lizards were essentially unrestrained. Hence, survival in Rock Valley was underestimated owing to movements of marked hatchlings. Also, none of the Mercury plots contained leopard lizards, which prey on *Uta*.

Between the summer of 1972 and the spring of 1973, minimal survival of hatchling *Uta* was evaluated in four areas in Rock Valley, where leopard lizards coexisted with *Uta*. Minimal survival in these plots ranged from 14 to 17%, with a mean of 15%. In contrast, minimal survival over this same interval in six Mercury plots was 43% (Turner et al. 1974).

Annual survival of older lizards

Here we examine annual survival of yearling and older *Uta* jointly. Survival of *Uta* was evaluated in 0.4-ha enclosures in Mercury Valley between 1969 and 1973. These data were summarized by Turner et al. (1974:Table 13).

Annual survival of yearling *Uta* ranged from 22% (1969–1970) to 53% (1971–1972), while annual survival of older *Uta* ranged from 11% to 37% in the same years. Survival of males and females over the 4-yr period was essentially identical (Turner et al. 1974:125). We did not analyze these data in terms of abiotic variables, but examined survival in individual plots as a function of initial spring densities (Fig. 2). The analysis of data from 18 plots (Turner et al. 1974:124) showed a highly significant inverse correlation ($r^2 = .46$, $F = 13.4$) between survival and spring densities ranging from 30 to 95 individuals/ha:

$$S_o = -0.0042d + 0.58 \quad (8)$$

As with hatchling *Uta*, survival of older lizards in the Mercury enclosures was better than that observed in Rock Valley (Turner et al. 1970). We have discussed our interpretation of this difference in connection with survival of hatchling lizards. During 1973 an experiment was carried out in Rock Valley. One 9-ha enclosure in Rock Valley (Plot 3) was subdivided with a fence into two 4.5-ha semicircles, and leopard lizards were removed from one of the semicircular areas. At the same time the density of leopard lizards was artificially increased to ≈ 2.5 individuals/ha in fenced Plot 1. Survival of older *Uta* between March and August 1973 in the area without leopard lizards was 40%. Survival over the same interval in Plot 1 was 15% (Turner et al. 1974).

A MODEL OF *UTA* POPULATION DYNAMICS*Modeling hatchling survival*

This portion of the model is based on three conclusions from foregoing studies: (1) survival rates (S_j) of male and female hatchlings are the same (2) there is no density effect on hatchling survival, and (3) the basic survival rate in the absence of leopard lizards (0.51) is reduced by the presence of this predator.

The experiment in 1972–1973 indicated that hatchling survival with leopard lizards present at a density of 2.5 individuals/ha was 35% of the survival rate in the absence of these predators (Turner et al. 1974: Tables 8 and 9). We now need to select some reasonable functional relationship between hatchling survival and predator density (D) so that if $D = 0$, $S_j = 0.51$,

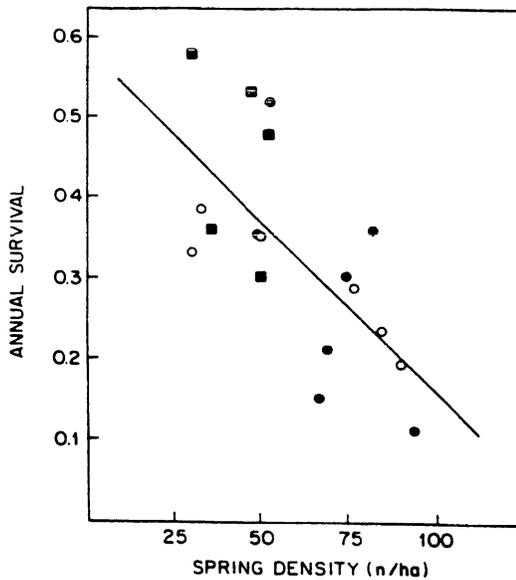


FIG. 2. Relationship between annual survival of adult *Uta stansburiana* and initial spring densities in 0.4-ha enclosures. Closed circles pertain to 1969-1970 and 1970-1971, squares to 1971-1972, and open circles to 1972-1973.

and if $D = 2.5$ *Crotaphytus*/ha, $S_j = (0.51)(0.35)$. Predator-prey interactions are customarily modeled as exponential, with the impact of predation proportional to the abundance of predators and the density of undiscovered prey (e.g., see Holling 1961; Eq. 9). To relate this concept to predator-induced mortality of hatchling *Uta*, we need to estimate a coefficient of "predator efficiency," α , such that $e^{-2.5\alpha} = 0.35$. Then $\alpha = 0.42$, and:

$$S_j = 0.51e^{-0.42D}, \quad (9)$$

with D the density (number per hectare) of leopard lizards. At leopard lizard densities ranging from 1 to 3 individuals ha, S_j ranges from 0.34 to 0.14.

Modeling survival of older *Uta*

This portion of the model is based on four conclusions: (1) survival rates of males and females are the same, (2) the basic (overall) survival rate (S_o) is inversely proportional to spring population density d , (3) the adjusted overall survival rate (S_{adj}) varies with the density of leopard lizards, and (4) yearling lizards have higher annual survival rates (S_y) than older lizards (S_o). The first step in estimating the annual survival rate of yearling lizards is to use Eq. 8. Data from the 1973 predation experiment indicated that adult survival between March and August in the absence of leopard lizards, and with a predator density of 2.5 individuals/ha was 40% and 15%, respectively (Turner et al. 1974). Hence, when $D = 2.5$, adult survival is only 37.5% of that in the absence of predators. Then, as with hatchlings, $e^{-2.5\beta} = 0.375$, and $\beta = 0.39$. Hence,

$$S_{adj} = S_o e^{-0.39D}, \quad (10)$$

with D the density (number per hectare) of leopard lizards.

We next estimated separate annual survival rates of yearling *Uta* (S_y) and older *Uta* (S_o) from S_{adj} , using experimental data from the Mercury plots. Average annual survival of yearlings in the plots was 36%, that of older lizards 25%. If S_o is equal to $0.694S_y$, and f_y is the fraction of the spring population composed of yearlings, then:

$$S_y = S_{adj}/(0.306f_y + 0.694). \quad (11)$$

The foregoing Eqs. 8, 10, and 11 take into account effects of *Uta* density and predation by leopard lizards in estimating death rates for two age-groups of adult *Uta* (yearlings and older lizards).

Although it is not biologically unreasonable to model the survival of yearling and older *Uta* separately, χ^2 tests of numbers of lizards of both age-groups surviving for 1-yr periods showed no significant differences in age-specific mortality rates. χ^2 totals for the four yearly periods analyzed ranged from 0.7 to 2.1 ($\chi^2_{.05} = 3.8$). Hence, we experimented with a simplification of the steps included in Eqs. 8, 10, and 11:

$$S_{adult} = 0.59e^{-0.39D - 0.0092d} \quad (12)$$

This expression incorporates effects of density and predation, but imposes equal survival rates on all *Uta* ≥ 8 mo of age.

Operating the survival section of the model depends on three initial state variables: (1) the density of the *Uta* population as of 1 March, d , (2) the proportion of the population composed of yearlings, f_y , and (3) the density of leopard lizards as of 1 March, D .

Annual survival rates of yearling and older *Uta* are converted to rates of loss per head per day, so that the state of the adult population can be tracked during the time that eggs are laid. For example, if S_y is 0.275 and S_o is 0.191, then daily loss rates, λ_y and λ_o , are 0.00353 and 0.00453, respectively. That is:

$$e^{-365\lambda_y} = 0.275. \quad (13)$$

Modeling egg production and recruitment

Numbers of clutches.—The number of clutches laid by 20+-mo-old females (F_o) is estimated with Eq. 3, and clutches laid by yearling females (F_y) with Eq. 2. Observations between 1966 and 1973 indicated that only a few females failed to produce at least one clutch of eggs. On the other hand, the maximum of clutches laid was seven (Medica and Turner 1976, Turner 1977). Hence, if either F_y or F_o is <1 or >7 , their values are taken as 1 and 7, respectively. If F_o is estimated as, say, 4.38 this is taken to mean that 62% of older females lay four clutches and 38% of them lay five. The relationship between number of clutches laid and dates of egg laying was modeled as follows: one clutch (20 April), two clutches (20 April, 25 May), three clutches

(15 April, 15 May, 15 June), four clutches (15 April, 15 May, 15 June, 1 July), five clutches (15 April, 10 May, 28 May, 15 June, 1 July), six clutches (15 April, 15 May, 30 May, 15 June, 30 June, 14 July), seven clutches (10 April, 25 April, 10 May, 25 May, 10 June, 25 June, 10 July). These dates were based on observations in 1966 and 1967 (Turner et al. 1970) and 1973 (Medica and Turner 1976).

Clutch size.—Average April clutch size of 20+-mo-old females is estimated using Eq. 4. Clutch sizes of older females for May and June are estimated from Eq. 5 and 6, respectively. Mean clutch sizes for yearling females for April, May, and June are estimated from corresponding clutch sizes of older females, using Eq. 7. If eggs are laid in July, the mean clutch size is taken as 2.6 (for females of any age).

Estimating egg production.—Age-specific estimates of clutch frequency determine how many clutches are laid (ordinarily n and $n + 1$) by yearling and older females, and what proportions of each age-group lay n and $n + 1$ clutches. The clutch frequencies determine the dates on which clutches are laid. Numbers of females alive on these dates are computed from initial numbers of each age-group alive on 1 March and from age-specific mortality rates. Numbers of females alive on each clutch laying date are multiplied by respective clutch sizes estimated for the date in question. Total egg production is derived by summation. Because no egg mortality is assumed, this number is taken as the summer recruitment by the population.

We attempted to avoid circularity in development of the model and subsequent evaluation of its performance by basing the model on data acquired in areas other than Plots 1-4 in Rock Valley. Egg production (Eqs. 3 and 4) and basic survival rates (Eq. 8) were estimated from data acquired in Mercury Valley. Only the functions for predation by leopard lizards were based on experiments in Plots 1 and 3 in Rock Valley.

In general, then, events in Rock Valley between 1966 and 1972 were independent of those on which the model was predicated.

How the model operates

To operate the model for 1 yr, or over a period of consecutive years, it is necessary to specify the following inputs: (1) the starting spring density of the population (number per hectare) as of 1 March, (2) the fraction of this population composed of yearling lizards, (3) the total rainfall (millimetres) between September and March for each year, with the understanding that the September-December rain occurred in the preceding year, (4) the average air temperature (degrees Celsius) in March for each year, and (5) the estimated spring density of leopard lizards (number per hectare) for each year.

Model function is illustrated with a brief description of computations for the year 1966-1967. The initial density (1 March 1966) was 56.8 lizards/ha, and the population was composed of 74% yearlings. Numbers of yearling and older females alive 1 March were, then, 21.0 and 7.4 individuals/ha. Winter rainfall was 139.1 mm, March air temperature 12°C, and leopard lizard density 2.94 individuals/ha. The basic adult survival rate was 34% (Eq. 8), and the adjusted annual survival (based on predator density) was $\approx 11\%$ (Eq. 10). Annual survival rates of yearling and older *Uta* were 12% (Eq. 11) and 8%, respectively. Survival of hatchlings was 15% (Eq. 9). The number of clutches laid by 20+-mo-old females was 4.42 (Eq. 3), by yearlings 3.70 (Eq. 2). Hence, older females laid either four or five clutches (between 15 April and 15 June, or between 15 April and 1 July), and yearlings three or four clutches (between 15 April and 15 June). April mean clutch size of older females was 4.98 (Eq. 4), of yearlings 4.01 (Eq. 7). The manner in which these data are combined to estimate total egg production is illustrated in Table 5. Total egg production was thus ≈ 240 . Of

TABLE 5. Estimated egg production and recruitment by *Uta stansburiana* in 1966. Numbers of females alive at time of egg laying, mean clutch sizes for that laying date, and egg production are indicated. Dual entries under May and June result from production of two clutches in the same month.

Age-group	Number of clutches laid	Measure	April	May	June	July	
Yearling	3	No. females	4.80	4.03	3.36	...	
		Clutch size	4.01	3.57	2.72	...	
		Total no. eggs	19.24	14.35	9.14	...	
	4	No. females	11.24	9.42	8.53	7.85	...
		Clutch size	4.01	3.57	2.72	2.72	...
		Total no. eggs	45.03	33.59	44.63	...	
Older	4	No. females	3.13	2.54	2.26	2.06	...
		Clutch size	4.98	4.31	3.04	3.04	...
		Total no. eggs	15.57	10.97	13.12	...	
	5	No. females	2.26	1.90	1.68	1.20	...
		Clutch size	4.98	4.31	4.31	3.04	2.60
		Total no. eggs	11.23	15.42	4.50	3.11	...

TABLE 6. Input variables used in a model of the dynamics of *Uta stansburiana* in southern Nevada.

Year	Spring <i>Uta</i> density d (n/ha)	Fraction yearlings f_v	Rainfall R (mm)	\bar{x} March temp. T (°C)	<i>Crotaphytus</i> density D (n/ha)
1966	56.8	0.74	139.1	12.0	2.94
1967			47.3	12.2	2.28
1968			88.2	11.6	1.72
1969			209.3	9.7	1.56
1970			83.3	10.1	1.67
1971			46.8	9.0	1.11

this number of lizards hatched, ≈ 37 (15%) survived until 1 March 1967. Survival of older lizards (6.22 individuals/ha) was the sum of surviving yearlings (42.03×0.12) and older lizards (14.77×0.08). The model thus predicted a density of ≈ 43 individuals/ha as of 1 March 1967, with 86% of the population composed of yearlings.

USING THE MODEL

Input variables, 1966–1971

The initial spring density (for the year 1966) was prescribed as 56.8 *Uta*/ha. This figure was the mean of the four values given for Plots 1–4 in the Appendix. The initial proportion of yearlings in the spring population (f_v) was taken as 0.74 (Turner et al. 1970). Amounts of rainfall between September and March and mean air temperatures in March for succeeding years were taken from records acquired by the Air Resources Laboratory (National Oceanic and Atmospheric Administration) in Las Vegas, Nevada. Densities of leopard lizards were mean densities in fenced Plots 1 and 3 in Rock Valley between 1966 and 1971 (see Turner 1975:117). Table 6 summarizes model input values.

Evaluating model performance, 1967–1972

The basic model generated population estimates for the years 1967–1972 as shown in Table 7. Table 7 also gives population estimates predicted by the simplified model (using Eq. 12 for adult survival). Actual mea-

TABLE 8. Comparisons of observed and predicted (basic model) attributes of *Uta* populations in southern Nevada, 1967–1972.

Attribute	Observed	Predicted
Mean density (n/ha), 1967–1972	41.4	37.8
Standard deviation of densities	20.8	13.6
Range of densities (n/ha)	23.5–80.3	21.7–57.8
Mean proportion of yearlings (f_v) in populations	0.78	0.78
Standard deviation of f_v	0.09	0.09

surements of *Uta* density in Rock Valley were available for the years 1966–1974. Densities for the years 1966–1973 are given in the Appendix, and the 1974 density (78.8 *Uta*/ha) was given by Medica and Turner (1975). Observed densities given in Table 7 are means of the values for Plots 1–4 in Rock Valley (see Appendix), except that overall means were adjusted downward in 1969 and 1971 when data were missing from Plots 1 and 3 (plots characterized by lower densities than observed in Plots 2 and 4). Table 7 also gives observed values of f_v (for 1967–1972) and values predicted by both versions of the model. Differences between the two model versions were nonsignificant. Other quantitative comparisons of actual observations and basic model projections are given in Table 8.

How well do numerical projections of the *Uta* models fit observations between 1967 and 1972? Fraleigh (1978) has suggested a test for comparing observations (y_i) and model predictions (\hat{y}_i). If \bar{y} is the mean of the observations, one computes $\Sigma(y_i - \bar{y})^2/n$, or MS_T ; $\Sigma(y_i - \hat{y}_i)^2/n$, or MS_E . The relative magnitude of these values is a measure of fit. If MS_E/MS_T is greater than one the model predictions do not "fit" observations as well as a straight line drawn through the mean of the observations. This test was applied to predictions of the *Uta* model, and the value of MS_E/MS_T was 1.25. The most conspicuous failing of the model was the prediction of a decline between 1966 and 1967, when *Uta* numbers actually increased appreciably. This 1 yr accounted for over 50% of the value of MS_E . The disagreement can be understood by comparing observations in Rock Valley in 1966–1967 with the ba-

TABLE 7. Comparisons of observed densities of *Uta stansburiana* in southern Nevada, and densities predicted by the basic population model and a simplified version of the model. Observed and predicted proportions of populations composed of yearlings (f_v) are also given.

Year	Observed mean density (n/ha)	Observed f_v	Basic model predictions		Simplified model predictions	
			Density (n/ha)	f_v	Density (n/ha)	f_v
1966	56.8	0.74
1967	80.3	0.84	43.0	0.86	43.6	0.86
1968	42.5	0.65	21.7	0.68	22.0	0.68
1969	34.6	0.78	24.9	0.78	25.2	0.79
1970	42.8	0.92	57.8	0.89	58.4	0.89
1971	23.5	0.74	45.5	0.78	46.3	0.77
1972	24.6	0.75	33.8	0.66	34.5	0.67

TABLE 9. Observed survival rates and egg production of *Uta stansburiana* in southern Nevada (1966–1967) contrasted with model estimates of these parameters.

Parameter	Model prediction	Observed value	Reference
Clutch frequency			
Older females	4.4	4.6	Turner (1977)
Yearling females	3.7	4.0	
Mean April clutch size			
Older females	5.0	4.4	Hoddenbach and Turner (1968)
Yearling females	4.3	3.7	
9-mo hatchling survival	15%	24%	Turner et al. (1970)
Annual yearling survival	12%	28%	Turner et al. (1970)
Annual survival, older lizards	8%	17%	Turner et al. (1970)

sic model predictions for that interval (Table 9). Although the model underestimated numbers and overestimated sizes of clutches somewhat, the important discrepancies lay in the drastically underestimated survival rates of lizards of all ages. In the model, these rates were strongly depressed by the high density of leopard lizards (2.94 individuals/ha) recorded in 1966. If observed survival rates for 1966–1967 (Turner et al. 1970) are combined with the initial density of the population as of 1 March 1966 (56.8 *Uta*/ha) and the model-estimated recruitment during the summer of 1967 (240 individuals/ha), the projected density as of 1 March 1967 is ≈ 72 individuals/ha, in good accord with what actually occurred.

Statistical performance of the basic model

We examined general properties of model function and the performance of the model over longer time intervals. In some tests input variables were modified; in others mathematical functions in the model were altered. All tests began with $d = 56.8$ *Uta*/ha and $f_v = 0.74$. For longer-term tests of stability and effects of density dependence, we used the 15-yr period 1964–1978 in Rock Valley and the 30-yr interval (1949–1978) for Lathrop Wells, Nevada, a community ≈ 18 km west of Rock Valley (Fig. 1). Rainfall and air temperatures in Rock Valley were measured by the Air Resources Board in Las Vegas, Nevada. Rainfall and temperature data for Lathrop Wells were drawn from climatological summaries for Nevada, and if data were unavailable for Lathrop Wells information for Beatty, Nevada, was used. Leopard lizard densities for these longer intervals were not known for either locale. For most tests we used artificial densities drawn randomly from a distribution ranging from 1 to 3 *Crotaphytus*/ha, with a mean of 2/ha. The probability of selecting a density of 1 or 3/ha was $\approx 2\%$, of selecting a density of 2/ha $\approx 28\%$. Densities of 1.2, 1.4, 1.6, 1.8, 2.2, 2.4,

2.6, and 2.8 *Crotaphytus*/ha had intermediate probabilities. For other tests we selected predator densities from distributions with lower means. This procedure is similar to that used by Pennycuick (1969) to synthesize estimates of beech mast crops used in tests of a population model of Great Tits.

Winter rainfall and March air temperature input variables were set at their mean values for the period 1964–1978 (107.22 mm and 10.2°C, respectively), leopard lizard density was set at 2 individuals/ha, and the model was used to predict changes during a 15-yr period. *Uta* densities declined exponentially and approached an asymptote of ≈ 33 individuals/ha after 13 yr. The asymptotic density was less than the mean density observed for the 9 yr 1966–1974 (47.5 *Uta*/ha).

When rainfall and predator densities were held constant and temperature varied, the model population declined in essentially the same manner, except that there was a 36% increase in numbers following a year in which the March air temperature was 19.3°. When predator density and temperature were held constant and winter rainfall permitted to vary, densities more than doubled when rainfall was >200 mm, and exhibited $\approx 40\%$ declines when rainfall was <70 mm. Densities were steady when rainfall was ≈ 100 mm. Amplitude of change was somewhat less when leopard lizard densities varied and rainfall and temperature were constant. In years when predator densities were high (2.6–2.8 *Crotaphytus*/ha) *Uta* numbers were reduced 30–40%; when predator density was low (1.2/ha) numbers increased $\approx 50\%$. When predator density was ≈ 2 /ha numbers remained steady. When March air temperature was varied and predator density and rainfall held constant, all mean air temperatures $<12^\circ$ resulted in decreases in numbers, the maximum decreases being $\approx 20\%$ when air temperatures were 5°–8°. Only a March air temperature of 19.3° resulted in a significant increase in numbers.

Fifteen-year tests were run in which winter rainfall was increased or decreased 50%, and leopard lizard densities increased 10 and 50% and decreased 10 and 50%. The model responded most conspicuously to 50% increases in predation and 50% decreases in rainfall, and model populations were essentially exterminated after 3 yr and 8 yr, respectively. Fifty-percent changes in predation had greater impacts on numbers of *Uta* than comparable modifications of rainfall had.

The model was stable over the 6-yr period 1967–1972, but we also tested it for intervals of 15 yr in Rock Valley and 30 yr at Lathrop Wells. All tests used actual abiotic data and predator densities selected randomly from symmetrical distributions with means ranging from 1.2 to 2 individuals/ha (Table 10). All three 15-yr runs using Rock Valley abiotic data exhibited good stability, but in no instance did the population rise much above the starting density of 56.8 *Uta*/ha. Because of this, mean model densities and standard deviations are less than those based on actual

TABLE 10. Results of 15- and 30-yr tests of a model of the dynamics of *Uta stansburiana* compared with actual observations in southern Nevada.

Source of data	Test number	No. years	Mean leopard lizard density D (n/ha)	Mean <i>Uta</i> density d (n/ha)	SD_d	Range of <i>Uta</i> density (n/ha)
Actual observations in Rock Valley (1966–1974)	...	9	...	47.5	20.8	23.5–80.3
Model, using Rock Valley abiotic data	1	15	2.0	22.9	9.4	12.1–49.1*
	2	15	2.0	32.6	12.9	17.3–58.6
	3	15	2.0	29.6	13.6	16.0–68.9
Model, using Lathrop Wells abiotic data	4	30	2.0	8.0	10.8	1.2–53.5*
	5	30	2.0	8.1	9.1	1.8–44.5*
	6	30	1.5	23.2	17.1	8.8–92.5
	7	30	1.2	50.7	20.6	25.3–112.5

* Excluding initial density of 56.8 *Uta* ha.

observations. In the Lathrop Wells tests using a mean predator density of 2 individuals/ha, projected *Uta* densities fell to <10 individuals/ha within 8 yr, and only the structure of the model prevented extinction (Table 10). In both tests, densities over the last 20 yr ranged from 2 to 9 *Uta*/ha. Table 10 also shows the results of two tests (6 and 7) in which predator densities were drawn randomly from distributions with means of 1.5 and 1.2 individuals/ha. At the lowest predator density, the model generated a series of *Uta* population estimates with statistical attributes similar to those of actual observations in Rock Valley.

The differences between Rock Valley tests 1, 2, and 3 and Lathrop Wells tests 4 and 5 stem from the lower winter rainfall at Lathrop Wells. Mean September–March rainfall in Rock Valley for the 15-yr period between 1964 and 1978 was ≈ 107 mm. Mean September–March rainfall at Lathrop Wells (or Beatty) for the 30-yr period 1948–1977 was 76 mm. The manner in which this difference affected the performance of model populations for the two localities may be understood by examining some of the demographic variables. Table 11 summarizes mean values for reproductive and survival variables for five tests. Because hatchling survival in the model is influenced solely by predator density, and because all simulations used synthetic predator densities drawn from the same distribution, one would expect similar hatchling survival rates for both localities. Because of the density-dependent component of adult survival, yearling *Uta* survived better in the Lathrop Wells tests because densities were always low after the first 8 yr. The better yearling survival in the Lathrop Wells simulations was more than offset by greater egg production in the Rock Valley tests. As can be seen from Table 11, both numbers of clutches and clutch sizes were greater in the Rock Valley simulations, and the differences were predominantly owing to greater winter rainfall in Rock Valley. Although the difference in individual egg production in the two populations was modest, it was enough to affect the performance of the model strikingly.

Density dependence in the model

Three tests examined the role of density dependence in the model. We used 30 yr of abiotic data from Lathrop Wells-Beatty for these tests, and predator densities drawn from a distribution with a mean of 1.2 individuals/ha, so that the model population could sustain numbers and exhibit normal amplitude. The basic case with which these three tests were compared was Test 7 (Table 10). In the first case, the density terms in Eqs. 3 and 4 were removed, so that egg clutch frequency and size were functions of rainfall and air temperature alone (Case 1). In the second (Case 2), the annual survival rate of adult lizards was set at 39%, instead of being computed as a function of density (Eq. 8). Adult survival was, however, still influenced by predator densities (Eq. 10). In the third, density-dependent influences on both egg production and survival were removed (Case 3). Year-to-year densities for Cases 1 and 2, and the basic case (Test 7 in Table 10) are illustrated in Fig. 3. The two tests in which one density-dependent constraint was removed (with the other operative) resulted in somewhat higher densities. When clutch size and frequency were density independent, model populations increased more during favorable periods but declined more abruptly during unfavorable times (Fig. 3). Model populations operating with either one of the two density-dependent

TABLE 11. Mean values (\pm one standard error) of four demographic variables in model-projected populations of *Uta stansburiana*. Test numbers are as in Table 10.

Test number	Mean number of clutches, older females	Mean April clutch size, older females	Mean annual survival, yearlings	Mean 9-mo survival, hatchlings
1	3.37 \pm 0.47	4.72 \pm 0.17	0.24 \pm 0.01	0.24 \pm 0.01
2	3.35 \pm 0.47	4.70 \pm 0.17	0.23 \pm 0.01	0.24 \pm 0.01
3	3.41 \pm 0.47	4.74 \pm 0.16	0.24 \pm 0.01	0.23 \pm 0.01
4	2.69 \pm 0.22	4.52 \pm 0.08	0.28 \pm 0.01	0.23 \pm 0.01
5	2.68 \pm 0.22	4.52 \pm 0.08	0.28 \pm 0.01	0.23 \pm 0.01

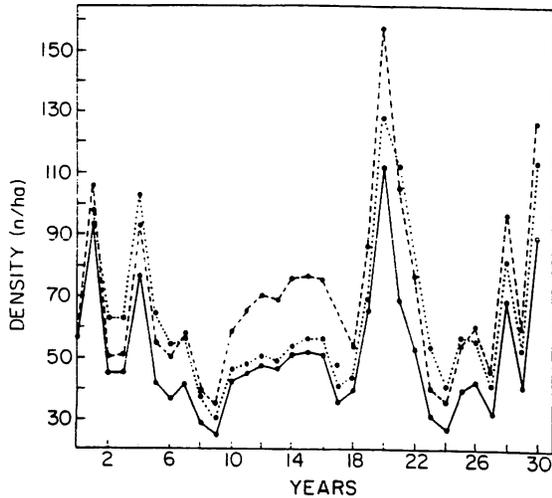


FIG. 3. Thirty-year tests of a population model of *Uta stansburiana* in southern Nevada. Solid line is the basic model (Test 7, Table 10). Dotted line is a model in which adult survival was constant, but egg production was density dependent. Dashed line is a model in which egg production was influenced by rainfall and temperature alone, but adult survival was density dependent.

mechanisms exhibited the same directions of change as the basic model and were stable over 30-yr periods. When both dependent mechanisms were removed, however, predicted numbers rose within 4 yr to unrealistically high levels (>120 *Uta*/ha) and ultimately exceeded 4000/ha. This outcome supports the inclusion of density terms in Eqs. 3 and 4, although *F* values for entry were statistically insignificant.

The foregoing results may be understood by examining the means of actuarial parameters associated with various versions of the model (Table 12). In Case 1, mean numbers and sizes of clutches were higher than in the basic version. This led to greater recruitment, higher densities, and reduced adult survival. The net effect of these changes was an apparently stable population with a modestly increased mean density. In Case 2, the basic adult survival rate was set at 39%, and adjusted survival rates of adults were slightly increased. Numbers and sizes of clutches laid were a bit lower because recruitment and population

sizes were higher. Again, the net interaction led to a stable population with a slightly higher mean density. When both density-dependent effects were removed, survival and egg production increased and the population rose to unrealistic levels.

DISCUSSION

The use of models to understand the functioning of animal populations and to shape further research has taken a variety of forms. These have included word models (e.g., Watson and Moss 1971), analyses of mathematical relationships between components of the dynamics of species (Watt 1963), submodels designed for use in a larger integrative model (e.g., Stenseth et al. 1977), and numerical models capable of predicting changes in numbers of animals. Examples of the latter are models of insect pests (e.g., Morris 1963, Menke 1973, Stinner et al. 1974, Hartstack et al. 1976), freshwater amphipods (Coulman et al. 1972), birds (Pennycuick 1969), foxes (Zarnock et al. 1975), and deer (Medin and Anderson 1979). None of the numerical models is capable of predicting >1 yr (or generation) in advance, but the performances of the amphipod and bird models have been tested with field data. The *Uta* model we have developed is most similar to that developed for Great Tits (Pennycuick 1969).

How well do numerical models of density changes perform? The *Uta* model failed remarkably in only 1 of the 6 yr for which observations and predictions were compared, and this could have been due to an error in estimating the density of a predator rather than to some failing in model mechanics. Other population models usually run into difficulty when such comparisons are made. When we applied Fraleigh's (1978) test to a model that predicts changes in numbers of a freshwater amphipod (Coulman et al. 1972), the value of MS_E/MS_T was ≈ 4.5 (cf. 1.25 for the *Uta* model). A similar test of the tit model developed by Pennycuick (1969) yielded a value of ≈ 1.7 . As we pointed out previously, Fraleigh's test is sensitive to a few big discrepancies. Just 2 yr (1951 and 1961) contributed over 50% of the value of MS_E for comparisons of observations and predictions of numbers of tits between 1947 and 1964. A model of a mixture of grasshopper

TABLE 12. Mean values of reproductive and survival parameters (\pm one standard error) generated by different versions of the *Uta stansburiana* population model. All means are based on 30-yr tests.

Model conditions	Basic adult annual survival rate (%)	Adjusted annual survival rate of yearlings (%)	Mean number of clutches, older females	Mean clutch size, older females	Annual recruitment (n/ha)
Basic case, test 7 (Table 10)	37 \pm 1	26 \pm 1	2.45 \pm 0.21	4.33 \pm 0.08	40 \pm 3.6
Case 1	30 \pm 2	21 \pm 1	2.74 \pm 0.22	4.56 \pm 0.07	58 \pm 5.0
Case 2	39 \pm 0	27 \pm 1	2.38 \pm 0.21	4.28 \pm 0.08	49 \pm 4.1
Case 3	39 \pm 0	27 \pm 1	2.74 \pm 0.22	4.56 \pm 0.07	628 \pm 158

species (in terms of biomass rather than numbers) tracked observations between May and August 1972 effectively, but diverged drastically during the months of September and October (Rodell 1977). One needs to consider other aspects of model predictions as well as absolute deviations. In the insect crop pest models, the most critical predictions are the times of numerical increases in the fields, and the exact numbers of insects to be expected during these peaks is less important. Simple agreement or disagreement in directions of change (aside from numerical accord) may also be instructive. In this respect, the *Uta* and amphipod models performed no better than would be expected by chance ($\approx 50\%$ accord), but the tit model predicted the right direction of change in 12 of 16 yr. Similarly, the grasshopper model tracked general trends almost perfectly. Two of the directional failures in *Uta* predictions occurred in years when observed numbers did not change conspicuously (1968–1969 and 1971–1972).

Fifteen- to 30-yr tests of the *Uta* model showed a general failure of model populations to sustain as high a mean density or as great a range in numbers as were actually observed between 1966 and 1974. Several tests showed that this problem was alleviated when predator densities were reduced. While such an effect could also be obtained by manipulating rainfall values, the tests were carried out with measured amounts of rainfall and synthetic values for predator densities. Hence, if one were to attempt further refinement and testing of the *Uta* model an indispensable step would be to measure predator densities accurately over a longer period of time.

The long-term tests using Lathrop Wells abiotic data were instructive, for they showed a clear-cut inability of the Rock Valley model population to survive a 30% reduction in mean winter rainfall. Yet *Uta stansburiana* exists at Lathrop Wells, and in even drier habitats in Death Valley. Hence, some features of the model are apparently site specific. The occurrence of *Uta* in these drier environments could be permitted by lower predation pressure or higher reproductive capacities. We would never expect the Rock Valley model to be applicable to *Uta* populations in, say, Texas or Colorado, for it is already known that these populations are characterized by different schedules of reproduction and survival (Tinkle 1967, Turner 1977:181). The Lathrop Wells tests suggest that the Rock Valley model may have even more restricted applicability. These considerations also imply that it would be risky to attempt to validate the Rock Valley model in any but relatively nearby areas.

The question of regulation of numbers of animals is still the focus of considerable inquiry, although perceptions of the problem have changed markedly since 1957 (Warren 1957). The lines of present thought may be inferred from some of the papers presented at the 1970 meeting at Oosterbeek, The Netherlands (den Boer and Gradwell 1971), and in a review by Lidicker

(1978). Natural regulation of lizard populations has been discussed by Turner (1977) and Ferguson et al. (1980). Here we will touch only on work with small sceloporines (Tinkle 1967, Ballinger 1976, Ferguson et al. 1980). One interesting point is that analyses of hatchling survival among Texas *Uta stansburiana* (Tinkle 1967, Fretwell 1972), Kansas *Sceloporus undulatus* (Ferguson et al. 1980), and Nevada *Uta stansburiana* (Turner et al. 1974) show no density-dependent effects. On the other hand, when adult *Urosaurus ornatus* were artificially removed from an area in New Mexico in July, the apparent survival of hatchling lizards was enhanced (Ballinger 1976). Ballinger has suggested that the improved survival of young lizards may reflect some form of competition between juvenile and older lizards. We have not examined this possibility for *Uta* because we lack reliable estimates of summer densities of adults. Recruitment of both juvenile *Uta* (Fretwell 1972, Turner 1977) and *Sceloporus undulatus* (Ferguson et al. 1980) seem to be influenced in a density-dependent manner. With *S. undulatus* the mechanism was postulated to be predation on egg-producing females; year-to-year variations in egg production were not believed to influence reproductive success significantly. With *Uta stansburiana*, on the other hand, analyses of Tinkle's data showed a significant inverse relationship between egg production and spring density. This relationship also emerged in the present study, and a mechanism was suggested. The Nevada *Uta* model also incorporates density-dependent effects on adult survival.

Pennycuick's (1969) evaluation of the tit population model showed that neither density-dependent fecundity nor density-dependent nest or winter survival could hold model predictions to levels observed in nature. Density-dependent juvenile survival, however, resulted in an asymptotic level almost exactly equal to the mean density of birds observed between 1947 and 1964. Tests of the *Uta* model led to contrasting conclusions. Both density-dependent adult survival and density-dependent fecundity controlled model population numbers, and at only slightly higher levels than observed. Only the removal of both influences led to unrealistic densities. We cannot compare the two models in terms of effects of density-dependent juvenile survival, because the *Uta* model did not include a density effect on the survival of hatchling lizards.

Pennycuick (1969:398) concluded that the fecundity relationships built into the tit model performed well, and that: "Calculated numbers of eggs fit well with . . . observed figures." Similarly, we believe that variables influencing frequency and size of *Uta* egg clutches were modeled more effectively than those affecting survival. In evaluating the general performance of the tit model, Pennycuick judged it "probable that some factor affecting mortality" had been omitted. In our view, the principal problem with the *Uta* model is also

of this nature. The process of survival was treated in a highly simplified manner. We assumed no egg mortality, which is inaccurate. This may not be a serious error, because K. S. Norris (*personal communication*) reported over 90% hatching of *Uta* eggs in laboratory experiments. We have no real understanding of post-hatching mortality except that ascribed to one species of predatory lizard. That there were other causes of mortality, apparently working in a density-dependent manner among adult *Uta*, seems clear from the experiments in small enclosures. The model assumes that the observed differences between survival in small enclosures (without leopard lizards) and survival among essentially unrestrained *Uta* coexisting with leopard lizards was due solely to the absence of the predator. The possible role of the enclosures themselves was not considered. The relationship between the prey species and the predator was modeled only in terms of density changes of the predator, but the impact of the predator would also be influenced by the density of the prey species, and possibly by social interactions among *Uta*. Finally, we did not assess the role of emigration in *Uta* populations. This is not as important an issue with *Uta*, a fairly sedentary species, as it is with more mobile species (e.g., moths and foxes).

Sinko and Streifer (1969) have emphasized how difficult it is to construct a realistic model by accurate experimental determinations of all model parameters, and encouraged the development of simpler models which can be used to test for important dependencies. Much of this has now been accomplished for *Uta stansburiana* in southern Nevada. Further development of the *Uta* model should emphasize experimental studies of factors influencing death rates. We postulate that, at least in southern Nevada, direct influences of abiotic variables are less important than predation.

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APPENDIX

Mean spring body masses (\pm one standard error) and densities (d , individuals per hectare) of yearling female *Uta* in four 9-ha areas in southern Nevada between 1966 and 1972.

Year	1			2			3			4		
	n	Mean body mass (g)	d	n	Mean body mass (g)	d	n	Mean body mass (g)	d	n	Mean body mass (g)	d
1966	18	2.04 (± 0.12)	51.9	27	2.04 (± 0.10)	72.6	20	2.22 (± 0.11)	35.6	11	2.06 (± 0.07)	67.2
1967	18	2.23 (± 0.09)	69.4	63	1.77 (± 0.06)	113.1	20	2.10 (± 0.08)	51.4	29	2.59 (± 0.07)	87.4
1968	14	3.26 (± 0.13)	38.0	16	3.03 (± 0.10)	63.2	7	3.33 (± 0.16)	25.7	8	3.17 (± 0.14)	43.0
1969	25	2.31 (± 0.13)	36.5	6	2.73 (± 0.12)	13.3	112	2.59 (± 0.05)	59.7
1970	22	2.56 (± 0.07)	34.4	36	2.20 (± 0.10)	54.1	20	2.59 (± 0.14)	31.6	35	2.29 (± 0.10)	51.2
1971	12	3.11 (± 0.09)	14.7	80	3.09 (± 0.05)	44.9	7	3.00 (± 0.11)	18.3
1972	3	3.51 (± 0.34)	13.3	31	3.37 (± 0.08)	37.9	26	3.08 (± 0.08)	24.6	5	3.24 (± 0.21)	22.5
Means		2.79 (± 0.24)	37.0 (± 8.8)		2.54 (± 0.23)	60.3 (± 10.1)		2.67 (± 0.20)	30.4 (± 5.2)		2.71 (± 0.17)	49.9 (± 9.3)