

# Comparative Ecology of Populations of the Lizard *Uta stansburiana*

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Various life history parameters of the iguanid lizard, *Uta stansburiana*, were studied over much of its geographic range, from southern Washington and Idaho to northern Sonora. Average body temperatures of active lizards are uniform throughout the range, but average time of collection is later in the north, indicating later emergence times and longer unimodal activity periods in the north. *Uta* utilize the "sit and wait" tactic of foraging, and are opportunistic feeders. Northern lizards eat primarily grasshoppers and crickets, beetles and ants, whereas southern ones contain beetles, termites, grasshoppers and ants, in order of volumetric abundance. Some seasonal and opportunistic dietary trends are described. Prey size shows little correlation with lizard head length, but larger-headed lizards generally eat more large prey than smaller lizards of the same sex in both north and south. Indices of estimated abundance and the total annual precipitation during the previous year are positively correlated, suggesting that abundance may be determined by food supply. In the north, females mature at smaller sizes and their average size is smaller. Average snout-vent length of all adults also increases from north to south, as does the degree of sexual size dimorphism ( $\delta > \text{♀}$ ). Predation on southern lizards is probably more intense, since both numbers and biomass of predatory animals and frequency of broken regenerated tails in *Uta* increase from north to south. Northern females generally lay one or two clutches of eggs during a 2-4 month oviposition period, while southern ones lay two or more clutches over oviposition periods as long as 5-6 months. Clutch size in the north is correlated with recent precipitation (during the preceding 6 months), and in the south with both date of collection (smaller clutches later in the year) and with snout-vent length (larger females lay larger clutches). Southern populations produce numerous clutches of small eggs, expend little energy on each individual progeny but produce many of them. Northern populations produce fewer clutches of large eggs, expend more energy on each individual progeny, and produce fewer offspring per year. Two southernmost populations exhibit some parallels with northern populations (small female size at maturity and relatively large eggs), suggesting some similarities in selective forces at both the northern and southern extremes of the species' range. As in the

teiid, *Cnemidophorus tigris*, the ecological challenges facing *Uta* in the north appear to be primarily climatic ones, whereas in the south biotic interactions (particularly predation and competition) assume relatively greater importance.

THE side-blotched lizard, *Uta stansburiana*, is ecologically one of the best known lizards in the world. Detailed autecological and demographic analyses of this species have been made in Texas and Colorado, at the southern and northern portions of the eastern border of its range (Tinkle, 1967, 1969a). Other studies of marked populations have been made in Nevada (Tanner and Jorgensen, 1963; Turner et al., 1970; Tanner, 1972), Utah (Tanner, 1965), California (Spoecker, 1967), New Mexico (Worthington and Arvizo, 1973) and Arizona (Parker, 1974). To date, there have been, however, only limited attempts to synthesize and explain latitudinal phenomena within the species, primarily with regard to clutch size (Tinkle et al., 1970; Fitch, 1970). Here we present data on relative abundance, time of activity, body temperature, diet, body size, broken tails and predation, and reproduction for specimens collected at 22 different localities between north latitudes of 28°20' and 46°50'. Our purpose is to amplify knowledge of latitudinal trends in these life history parameters for comparison with other lizard species studied similarly (Pianka, 1970), to delimit probable factors causing observed trends, and to compare our results with other studies. Previous studies have shown that wide variations exist in parameters such as mean life expectancy, aggressive behavior, home range size, population density and clutch size, not only at different latitudes but also at different altitudes at the same latitude, and from year to year or within one year at the same general location. The large number of variables influencing life history parameters in this species thus makes difficult an analysis on a comparative population basis over the species' wide geographic range. An analysis of the degree of influence of various density-independent and density-dependent factors should, however, contribute to a better understanding of the mechanisms by which this widespread species has successfully exploited the flatland desert environments of western North America.

#### STUDY AREAS AND METHODS

Observations were made on 3792 individuals of *Uta stansburiana* between 1962 and 1972 on

22 geographically separate flatland desert study areas (Table 1). Much of our information is based on 2111 specimens which were actually collected and preserved (now deposited at the Los Angeles County Museum of Natural History), although abundance estimates, activity patterns, broken tail percentages and body sizes also incorporate 1068 animals that were not preserved and/or 570 recaptures of 613 animals that were marked and released. Climatic data, fauna, and flora for most of the study areas have been published (Pianka, 1965, 1966, 1967, 1970; Parker, 1971, 1972a, 1974; Pianka and Parker, 1972).

At South Mountain, Arizona, live lizards were trapped, marked by toe-clipping and released; others were collected and preserved. In other areas, lizards were observed while observers walked transects through the habitat, recording distances covered with leg pedometers. Estimated indices of abundance were converted from the number per man-mile to the approximate number per hectare (Pianka, 1970; Pianka and Parker, 1972). For most lizards encountered, we recorded date, time, approximate size (small, medium or large), sex (if possible) and microhabitat position in the environment when first sighted. Lizards actually collected provided additional data on cloacal temperature, gonadal condition, wet weight, exact size (snout-vent length, or SVL) and whether or not the tail had been broken and regenerated. All SVL and tail lengths were measured to the nearest mm with plastic or metal rulers on live or freshly killed lizards in the field before preservation. Broken tail data include the first capture in each size group for mark-release animals, and exclude lizards with tails broken in collection or handling. Average adult SVL's include only first captures of mark-release lizards. Head lengths (the distance from the anterior edge of the ear opening to the tip of the nose) were measured to 0.1 mm with vernier calipers on preserved specimens. Dissection of these preserved lizards supplied information on gonadal state and stomach contents. Testicular dimensions of preserved specimens were measured with vernier calipers to the nearest 0.1 mm. Oviparous females (those with eggs in their oviducts) and their eggs were weighed to the nearest 0.1 g with

TABLE 1. COLLECTION SITES OF *Uta stansburiana* USED IN THIS PAPER.

Location	Letter Code	Latitude	Year(s) of Collection
"Northern" areas			
1. 3 km S Beverley, Washington	W	46°50'	1962
2. 60 km S Mountain Home, Idaho	I or N	42°36'	1962
3. Hart Mtn. National Antelope Refuge, Oregon	H	42°25'	1962
4. Sulfur, Nevada	Su	40°48'	1972
5. Stansbury Island, Utah	U1	40°47'	1963
6. 3-4 km W Grantsville, Utah	U2	40°36'	1970-72
7. 8 km N Lovelock, Nevada	L	40°12'	1964
8. 8 km S Gabbs, Nevada	G	38°48'	1964
9. 40 km NW Beatty, Nevada	V	37°05'	1964
10. Rhyolite, Nevada	Rh	36°55'	1972
"Southern" areas			
1. ~ 10 km W Pahrump, Nevada	P	36°18'	1964
2. Kyle Canyon, Nevada	K	36°15'	1972
3. 17 km SSE Searchlight, Nevada	S	35°18'	1964
4. 8 km N Mojave, California	M	35°06'	1963-64
5. 12 km N Topock, Arizona	To	34°46'	1972
6. 22-23 km E Twentynine Palms, California	T	34°07'	1964
7. 29 km SE Salome, Arizona	R	33°41'	1963-64
8. Phoenix South Mountain, Arizona	SM	33°26'	1965-66
9. 16 km NW Casa Grande, Arizona	C	32°57'	1963-64
10. 1-75 km W El Paso, Texas Dona Ana & Luna Counties, New Mexico	EP	31°50'	1970
11. 40 km SE Puerto Libertad, Sonora, Mexico	B	29°38'	1969
12. 7 km E Estero de Tastiota, Sonora, Mexico	A	28°20'	1969

a Pesola spring balance. The term "reproductive effort," although recognized to have broader implications, is used here as total oviducal egg weight/total weight of ovigerous female. "Expenditure per progeny" correspondingly refers to weight of one egg over the total weight of an ovigerous female. Ballinger and Clark (1973) demonstrated that such ratios are comparable to the same ratios for dry weight, and are functional measures of reproductive

effort. Volumes of intact stomachs were estimated to 0.1 cc using a small narrow-necked graduated cylinder and volume displacement. Estimates were made of the numbers and volumes of items in various prey categories for each stomach. Approximate volumes in  $\mu$ l of individual prey items were estimated visually by the proportion of the total stomach volume taken up by a given item. Prey items in each lizard stomach were counted individually, ex-

TABLE 2. STATISTICS ON TIME OF ACTIVITY, AIR TEMPERATURE AND BODY TEMPERATURE OF *Uta* COLLECTED PRIMARILY DURING SUMMER.

Area	Time of collection <sup>a</sup>				Air temperature				Body temperature			
	$\bar{x}$	S	N	SE	$\bar{x}$	S	N	SE	$\bar{x}$	S	N	SE
N	11.88	3.79	13	1.05	25.85	3.62	13	1.00	35.56	2.23	14	0.60
U71	11.84	1.15	112	0.34	22.50	6.09	9	2.03	35.46	2.16	16	0.54
L	12.46	4.59	79	0.52	26.58	4.65	69	0.56	34.78	2.00	88	0.21
G	11.06	3.14	33	0.55	25.22	3.53	28	0.67	35.47	1.98	31	0.36
V	12.03	4.32	27	0.83	27.30	3.51	32	0.62	35.00	1.53	31	0.275
P	10.58	4.12	14	1.10	26.95	3.80	17	0.92	34.79	1.76	20	0.39
S	9.92	3.70	34	0.64	29.15	2.00	58	0.26	34.59	2.49	62	0.316
M63	9.70	2.00	114	0.19	27.11	3.04	111	0.29	35.69	2.11	109	0.202
M64	10.35	1.58	17	0.38	25.53	5.71	17	1.38	34.05	7.99	15	2.064
T63	9.27	0.16	3	0.90	28.07	1.46	3	0.85	36.20	2.36	3	1.361
T64	9.35	1.03	6	0.42	20.91	7.43	7	2.81	36.40	1.72	6	0.702
R63	9.90	2.50	23	0.52	26.82	4.08	21	0.89	35.95	1.84	23	0.384
R64	9.32	1.49	20	0.33	22.55	2.71	20	0.61	35.84	1.85	20	0.413
SM65	Summer	12.08	4.36	59	0.57	—	—	—	—	—	—	—
	Winter	14.16	2.14	73	0.25	22.88	5.50	32	0.97	—	—	—
C63	9.90	2.51	143	0.21	27.99	4.29	113	0.40	35.84	1.67	135	0.144
C64	10.20	3.21	144	0.27	24.00	5.06	145	0.42	35.19	2.20	141	0.185
North	11.95		264		25.61	—	151	—	35.21	—	180	—
South	10.60		650		25.92	—	554	—	35.55	—	534	—

<sup>a</sup> In hundredths of an hour.

cept for termites for which standards were determined and the number per stomach estimated from the volume. In some of the following analyses, we use the length of the growing season (Anonymous, 1941; Visher, 1954) as a more accurate indicator of climatic differences between study areas than latitude. Methods employed are discussed in greater detail by Pianka (1965, 1967, 1970).

#### DAILY ACTIVITY PATTERN, AIR TEMPERATURE AND BODY TEMPERATURE

Air and body temperature statistics are remarkably uniform throughout the range of this species (Table 2), and are similar for juveniles and adults, and for both sexes (Pianka, 1965). In keeping with the constancy of body and air temperatures, average time of collection of *Uta* is later in the north than in the south, changing more or less continuously with latitude; moreover, variance in time of collection is significantly greater in the northern deserts. Thus daily activity periods of northern utas are probably longer, presumably because unimodal activity periods and later initiation of activity occur through much of the year in the north, while bimodal periods and earlier activity are the rule in the south. The discrepancy for the

southern area at South Mountain, Arizona, is due to more intensive evening collecting, raising the mean collection time; bimodal activity was centered around 0900 in morning, and 1730–1830 in evening, resulting in the high mean as compared to other southern areas where evening collections were not made. The unimodality of daily activity in southern areas during winter is reflected in the high mean and low variance for area SM utas in the winter (Table 2). When activity is expressed as time since sunrise, *Uta* is active significantly earlier than 3 other sympatric species (Pianka, 1973).

The latitudinal pattern for *Uta* activity and body temperatures contrasts with that of *Cnemidophorus tigris*, which is active at similar times in north and south, but has a lower mean body temperature in the north (Pianka, 1970). By thus shifting their activity periods, northern *Uta* maintain relatively constant body temperatures throughout a day, while northern *Cnemidophorus* are active during similar periods as in the south, but at slightly lower body temperatures (Pianka, 1970).

#### FOOD AND FEEDING

*Foraging behavior.*—Iguanids in general and *Uta* in particular usually use the "sit and wait" tactic

TABLE 3. SUMMARY OF STOMACH CONTENTS OF 556 *Uta* FROM FIVE STUDY AREAS IN THE GREAT BASIN DESERT (AREAS I, L, G, U2 AND V).

Prey Category	Number	Volume (cc)	% Total Number	% Total Volume	Frequency
Spiders	129	4.70	4.7	6.6	25.7
Solpugids	5	.56	.2	.8	1.1
Ants	1331	7.87	48.8	11.1	33.5
Other Hymenoptera	27	.54	1.0	.8	4.0
Grasshoppers & Crickets	194	21.68	7.1	30.5	33.8
Roaches	2	.20	.1	.3	.4
Mantids	3	.66	.1	.9	.5
Beetles	354	12.35	13.0	17.4	37.6
Termites	45	.10	1.7	.1	.2
Homoptera-Hemiptera	247	2.19	9.1	3.1	21.2
Diptera	41	2.54	1.5	3.6	8.3
Lepidoptera	12	1.24	.4	1.8	2.3
Insect larvae	109	6.13	4.0	8.6	15.1
Unidentified					
Insects	226	6.52	8.3	9.2	23.0
Plant Materials		.89		1.3	2.7
Unidentified					
Material		2.89		4.1	11.0
	2725	71.06			

of foraging much more than, for instance, do teiid and scincid lizards (Pianka, 1966, 1969, 1970, 1973). *Uta* often perch on small rocks or logs (if present) thus increasing their height above the ground and presumably enlarging their effective foraging area. However, in the flatland desert, there are usually very few rocks, and *Uta* are generally found on the small mounds around the bases of nearly any species of perennial plant (larger bushes with larger mounds seem to be preferred), often basking in the sun under the shrub, waiting for a suitable prey item to make an appearance. From this position, *Uta* make short dashes to capture fairly active prey types moving past or alighting nearby, such as arachnids, beetles, and grasshoppers. They were observed to stalk large grasshoppers, at first walking slowly towards the insect, then making a short, very swift attack. Occasionally, more active foraging methods are employed, and the species has been observed to climb up into bushes a foot or so for some particularly enticing food item. Some digging for prey was observed, but by far the most prevalent method of foraging in the flatland desert is by sitting and waiting more or less passively underneath a desert shrub.

*Northern versus southern diet.*—Major items in the diet of *Uta* have been previously listed for Utah (Knowlton, 1938; Knowlton and Anthon, 1935; Knowlton and Janes, 1932; Knowlton and Thomas, 1936) as leafhoppers, grasshoppers, ants and leafbugs; for Texas (Tinkle, 1967) as beetles, ants, bugs and grasshoppers; and for southern New Mexico (Dixon and Medica, 1966) as beetles and ants. Our samples mostly contain the same major food items, but there is a moderate latitudinal shift in the composition of the diet. Northern lizards take grasshoppers and crickets, beetles, ants and insect larvae in order of percent of total volume (Table 3). Southern utas, like southern *Cnemidophorus tigris* (Pianka, 1970), eat large numbers of termites, with prey items in the sequence: beetles, termites, grasshoppers, ants and insect larvae (Table 4). These samples are composed primarily of stomachs from one northern (Grantsville, Utah) and one southern area (Casa Grande, Arizona), which collections were made throughout most of a year and at different times of day. Such collection techniques, plus the large sample sizes, should reduce or eliminate any bias arising from differences between areas or in daily or seasonal activity.

TABLE 4. SUMMARY OF STOMACH CONTENTS OF 811 *Uta* FROM SEVEN SOUTHERN STUDY AREAS (P, S, M, T, R, C AND SM) IN THE MOJAVE AND SONORAN DESERTS.

Prey Category	Number	Volume (cc.)	% Total Number	% Total Volume	Frequency
Spiders	76	4.1	.9	2.6	6.2
Mites	24	trace	.3	trace	.3
Solpugids	2	.5	trace	.3	.3
Collembolla	90	trace	1.1	trace	.4
Ants	2459	14.7	30.5	9.2	33.2
Other Hymenoptera	27	2.6	.3	1.6	2.8
Grasshoppers	158	19.3	2.0	12.1	13.6
Roaches	28	3.6	.4	2.3	2.3
Mantids	7	1.3	.1	.8	.9
Adult Ant Lions	5	.6	.1	.4	.6
Beetles	960	41.2	11.9	25.8	46.6
Termites	3115	33.8	38.7	21.2	22.2
Homoptera-Hemiptera	248	1.9	3.1	1.2	4.6
Diptera	34	.4	.4	.3	3.2
Lepidoptera	21	1.2	.3	.8	1.1
All Larvae	191	11.3	2.4	7.1	12.0
Unidentified					
Insects	417	9.9	5.2	6.2	25.2
Insect Eggs	63	.3	.8	.2	.6
Insect Pupae	2	trace	trace	trace	.3
Lizards	2	.5	trace	.3	.3
Plant Materials	122	3.0	1.5	1.9	4.0
Unidentified					
Materials		9.4		5.9	23.2
	8051	159.8			

There is little difference between northern and southern populations in dietary diversities based on either numbers or volumes of the various prey categories. Northern males, however, have slightly more diverse diets than northern females, while southern females take a broader variety of foods than southern males. Pianka (1970) found a significant negative correlation between food species diversity by volume and short term (previous 5 years) precipitation in *Cnemidophorus tigris*. No such correlation exists between food species diversity (by volume) and precipitation during the year prior to study in *Uta*.

*Seasonal changes in diet and prey size.*—Tinkle (1967) showed that the diet of utas changes seasonally and between years and microhabitats, at least partially as an opportunistic response to availability of different prey species. Two of our areas, one northern (Grantsville, Utah) and one southern (Casa Grande, Arizona), have sample sizes large enough for seasonal analysis

(Figs. 1, 2). Five major food items dominate the northern diet: grasshoppers, crickets, ants, beetles and spiders. Crickets and spiders are prominent prey in spring, grasshoppers in summer, and ants and beetles in the autumn. On the southern area, ants and beetles are again important food items, here during most of the sampling period. Grasshoppers, crickets and spiders are of little importance, whereas termites assume a major proportion in most samples. The 7 August sample nicely illustrates the opportunistic feeding habits of *Uta*; termites were swarming and constituted 92% of the food by volume on this day, whereas during the four preceding days (3–6 August), termites comprised only 30% of the diet. Seasonal dietary patterns in northern and southern *Uta* are similar to those of northern and southern *Cnemidophorus tigris* (Pianka, 1970), which species differs primarily by taking fewer grasshoppers and more termites in the south.

Seasonal changes in prey size generally parallel those in taxonomic composition of the prey.

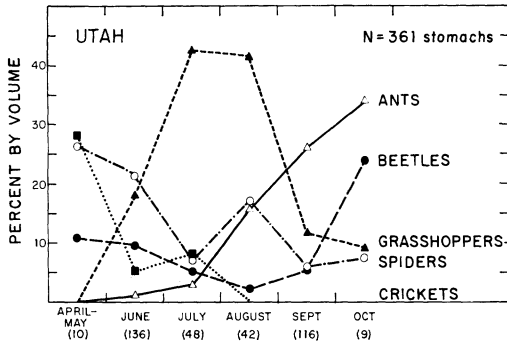


Fig. 1. Seasonal changes in the diet of *Uta stansburiana* from Grantsville, Utah (area U2).

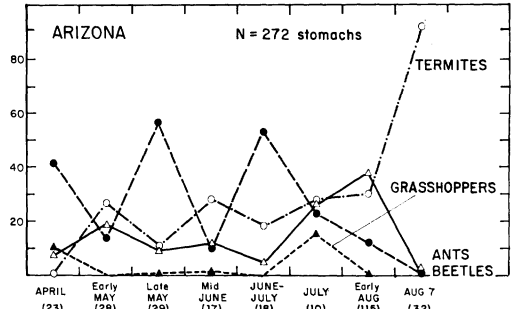


Fig. 2. Seasonal changes in the diet of *Uta stansburiana* at Casa Grande, Arizona (area C). Vertical axis plots percentage of diet by volume among four prey taxa indicated.

Southern animals (Casa Grande, Arizona) follow a pattern of medium-large prey in spring, small prey in summer, and medium prey in late summer (Table 5). Northern utas (Grantsville, Utah) eat large prey in spring and summer, medium prey in later summer and small prey in autumn. In the north, late summer and autumn decreases in prey size are paralleled by decreases in mean head lengths, but there are no consistent significant correlations between head length and prey size in either north or south.

Generally, larger prey sizes in the north seem related to presence of more large prey types (crickets and grasshoppers) in spring and summer. Small prey may not be as available to northern utas as they are to southern ones during spring and summer. Alternatively, utas might be taking smaller prey in the south due to the large number of larger sympatric iguanids, which could eat more of the large prey fauna than in the north.

TABLE 5. SEASONAL CHANGES IN PREY SIZE AND CORRELATIONS BETWEEN HEAD LENGTH AND PREY SIZE IN ONE NORTHERN AND ONE SOUTHERN POPULATION OF *Uta stansburiana*.  $r_1$  = head length categories versus mean volume of prey eaten by lizards with that head length;  $r_2$  = each lizard's head length versus the mean volume of its prey;  $r_3$  = prey size versus head length for all prey items.

Month	N	$\bar{x}$ head length (mm)	$\bar{x}$ prey size (cc)	N prey	$r_1$	$r_2$	$r_3$	$\bar{x}$ prey/stomach
(AREA U2)								
Apr-May	6	10.5	.027	19	.100	.126	-.057	3.2
Jun	94	10.8	.025	317	-.057	-.011	.023	3.4
Jul	34	10.9	.041	75	.404*	.249	.239	2.2
Aug	32	9.2	.013	130	.498**	.526**	.414***	4.1
Sep	87	9.6	.007	849	.284**	.278*	.005	9.7
Oct	6	9.4	.004	55	-.308	-.308	-.243	9.2
(AREA C)								
Mar 64	7	11.1	.014	63	-.352	-.317	-.048	9.0
Apr 64	52	11.0	.030	256	.361**	.229	.231**	4.9
May 63	19	10.7	.015	321	.510*	.439	.379***	16.9
Jun 63	13	10.4	.009	292	.237	.189	.040	22.4
Jul 63	10	11.1	.004	560	.479	.527	.273***	56.0
Aug 63	129	8.3	.012	3139	.325**	.144	.155***	24.3
Aug 64	15	10.6	.014	121	.389	.393	.207*	8.1

Significance Levels: \* =  $P < .05$   
 \*\* =  $P < .01$   
 \*\*\* =  $P < .001$

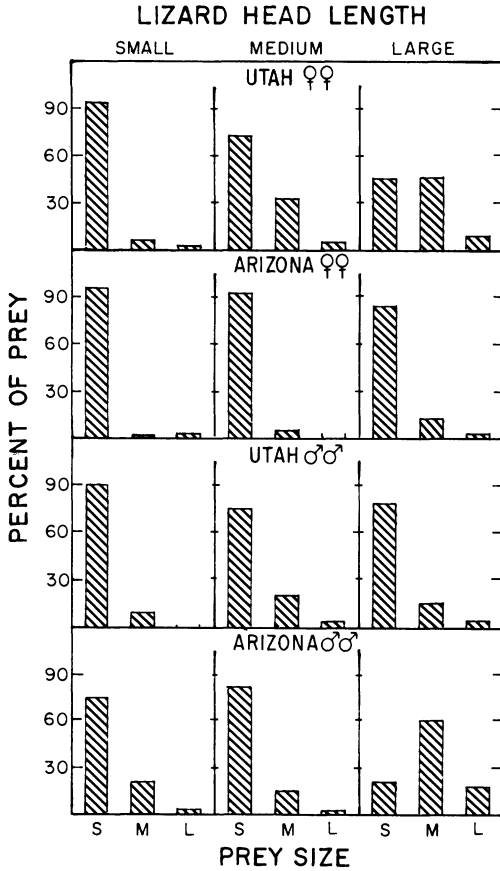


Fig. 3. Composition of diet comparison between small (.001-.014 cc), medium (.015-.064 cc) and large (.065-.724 cc) prey size groups and 3 head length groups of male and female *Uta stansburiana* from a northern (Grantsville, Utah) and a southern study area (Casa Grande, Arizona).

*Prey size and head length.*—Fig. 3 shows frequencies of prey size groups by head length group and sex for two localities, one northern and one southern. Utah females show a significant progressive increase in number of larger prey with increasing head length. Arizona females exhibit no significant differences among head length groups. Mean number of prey per stomach is inversely correlated with head length. Larger females generally eat a few large food items while smaller females eat many small items. Trends are less pronounced among males. In Utah males, the frequency of larger food items increases only slightly with increasing head length, while the largest Arizona males eat mostly medium and large prey. Comparisons between the sexes reveal reverse trends in the two geographic areas. Utah lizards, with

little sexual size dimorphism, differ in that larger females eat more large food items than small females and males, whereas males differ only slightly between head length groups. Among Arizona lizards, which have the most marked sexual size dimorphism (below), females eat the smallest food items almost exclusively, while all groups of males, especially the large group, eat more of the larger food items. Samples from near El Paso, Texas, show similar sexual dimorphisms in food habits.

In island *Anolis*, sexual size dimorphisms are pronounced, with larger lizards eating larger prey, presumably reducing dietary overlap between the sexes (Schoener, 1967, 1968). One might therefore expect utas to exhibit "ecological release" and have greater sexual dimorphism and a wider "between phenotype" component of food niche breadth (Roughgarden, 1972) where they coexist with fewer sympatric iguanids, as in Utah. Utah lizards, however, do not take a wider variety of prey than Arizona lizards (either by taxon or size), where there are more sympatric iguanids (6 vs 4). Many factors may be involved. The increase in larger prey in large Utah females may stem from the presence of fewer related competitors, but exactly why females rather than males are using these larger prey items remains conjectural. Alternatively, the Utah results may be misleading since a very similar, slightly larger, sympatric species (*Sceloporus graciosus*) on the Utah area may influence the size distribution of available prey. A similar closely related species (*Urosaurus graciosus*), however, occurs on the Arizona study area. The large prey of the large Arizona males may be the result of their being in a size class by themselves; they are larger than any other lizards in the samples and may be able to take larger prey purely because of physical factors. Further conclusions are impossible due to inadequate information on the spectrum of available prey sizes on the two geographic areas. The much larger number of prey per lizard stomach in Arizona than in Utah (Table 5) may reflect such differential availability and perhaps also differences in body size (Arizona lizards are larger and should have larger stomachs, which would hold more food items). Avery (1973) found an isometric relationship between stomach volume and body weight in *Lacerta vivipara*. A low average number of prey per stomach within a geographic sample indicates that more large prey items are eaten, although this relationship need not hold between Arizona and Utah.



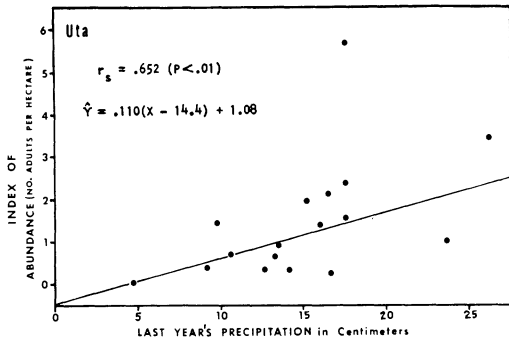


Fig. 4. Indices of estimated abundance of *Uta stansburiana* plotted against total precipitation during the year prior to the time of the estimate.

#### ABUNDANCE

There is no latitudinal trend in either peak or average estimated indices of abundance of *Uta*, but there is a statistically significant correlation with recent precipitation (Fig. 4). Specifically, the best correlation ( $r_s = .652$ ,  $p < .01$ ) was obtained with the total precipitation of the previous year, which is what one would predict, since most of the lizards are probably less than a year old judging from population studies (Tinkle, 1967). Food supply, one factor controlling abundance, is presumably strongly influenced by precipitation (Hoddenbach and Turner, 1968). Thus *Uta* differs from *Cnemidophorus tigris*, whose abundance is correlated with the last five years' precipitation better than with that of the last year (Pianka, 1970). This difference is in the direction one would expect since *Cnemidophorus* is a relatively long-lived lizard compared to *Uta* (Turner et al., 1969).

#### BODY SIZE

*Minimal size at sexual maturity (females).*—We use the smallest gravid females to indicate minimal size at sexual maturity. Maturity is generally attained at a small size in *Uta* populations occurring on areas with a short growing season. Among our northern areas, minimal size is directly correlated with length of the growing season, whereas in southern populations no such correlation exists. Southern utas, however, generally mature at larger sizes than northern ones. The only exceptions are our two southernmost areas whose exceptional nature is discussed below. Tinkle's (1967) data for Texas are similar to southern New Mexico (EP), but his Colorado data do not fit the pattern ob-

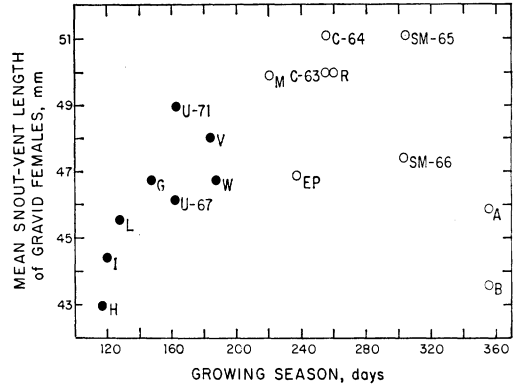


Fig. 5. Mean snout-vent length (mm) of gravid female *Uta stansburiana* plotted against growing season. Spots = northern areas ( $r = .71$ ,  $P < .05$ ); circles = southern areas ( $r = -.63$ ,  $P < .05$ ).

served for northern lizards in our data. It can safely be assumed, however, that female utas mature at smaller sizes in areas with relatively short growing seasons (the smallest gravid female was 37 mm), allowing reproduction during their first breeding season. Since areas with short growing seasons allow only limited periods for growth after hatching, selection has apparently favored early maturity at a small size, rather than later maturity (in second breeding season) at a larger size (Tinkle, 1967).

Average size of gravid females was also compared with growing season for each area (Fig. 5). Again, there is a significant positive correlation for northern areas ( $r = .71$ ,  $p < .05$ ) and a significant negative correlation ( $r = -.63$ ,  $p < .05$ ) for southern ones. Average sizes are small in northern areas with short growing seasons and in the two Sonora areas. In northern areas with relatively longer growing seasons and in all other southern areas, average size is larger. This reflects the longer favorable period for growth in these areas. Female utas evidently must reproduce at smaller sizes at the extremes of the species' range; in the north because of a short season favorable to activity, and in the extreme south because of some other, as yet unknown, limiting factor. The close phylogenetic relationship between *U. taylori* (Ballingier and Tinkle, 1972), whose distribution is near our Sonora collection sites, and *U. stansburiana* of the Great Basin could be responsible for reproductive similarities between extreme northern and southern populations noted here and later. These patterns are further complicated by wide annual variations in average size

TABLE 6. AVERAGE BODY LENGTHS (SVL) OF ADULT MALE AND FEMALE *Uta stansburiana* FROM 10 LOCALITIES.

Area	Latitude	Month	Year	N	Male ( $\geq 45$ mm)		Female ( $\geq 43$ mm)		
					$\bar{x}$	Range	N	Range	
H	42° 25'	Jun-Jul	62	47	47.55	45-53	25	45.04	43-49
U2	40° 36'	Apr-Aug	71	107	48.56	45-54	104	48.72	43-54
U2	40° 36'	Mar-Jun	72	20	48.35	45-55	22	48.36	44-55
L	40° 12'	Jul-Aug	64	27	48.26	45-54	36	46.53	43-52
K	36° 15'	Apr	72	18	48.22	45-52	26	45.15	43-50
M	35° 06'	May-Aug	63	55	51.85	45-56	59	49.56	44-58
SM	33° 26'	Jan-Jul	65	50	53.80	46-62	49	49.84	43-56
SM	33° 26'	Jan-Jul	66	102	51.71	45-58	114	47.39	43-55
C	32° 57'	Apr-Aug	63	63	54.94	49-64	84	50.08	43-58
C	32° 57'	Mar-Aug	64	101	55.34	48-61	96	51.11	47-56
EP	31° 50'	May-Aug	70	18	50.39	47-53	16	47.44	44-50
B	29° 38'	Jun	69	10	48.60	45-53	8	44.37	43-46
A	28° 20'	Jun	69	17	53.29	50-57	21	47.05	44-50

of gravid females at the same locality (areas SM and U2).

*Latitudinal patterns in adults.*—Soulé (1966) found a significant negative correlation between body size of *Uta* and number of sympatric iguanid species on islands in the Gulf of California, Mexico. He reasoned that presence of fewer sympatric iguanids allows *Uta* greater ecological amplitude, reflected by increased body size. Tinkle (pers. comm.), however, used larger samples and found no significant correlation. Our data for continental populations show a significant *positive* correlation between body size and number of sympatric iguanids, the reverse of Soulé's results for islands (Table 6,

Fig. 6). Average body size is also, however, significantly correlated with growing season, most strongly in males. In continental populations, there is thus apparently little real correlation between body size and number of sympatric iguanids, particularly since most sympatric species are larger than *Uta*, suggesting that these lizards would be smaller where there are many sympatric species. Additionally, lizard species diversity is correlated both with plant volume diversity and with growing season length (Pianka, 1967). The correlation of *Uta* body size with growing season suggests that longer periods favorable for growth at critical periods of early growth allow attainment of larger average sizes for both sexes. Greater survivorship of adults in populations with large average size is unlikely, since population studies have shown that *Uta* in areas with relatively short

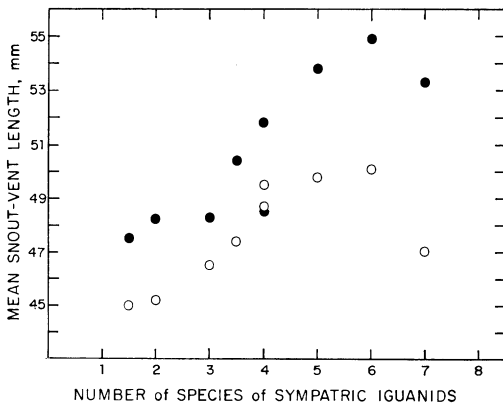


Fig. 6. Mean snout-vent lengths (mm) of adult *Uta stansburiana* plotted against the number of sympatric iguanid species. Spots = males; circles = females.

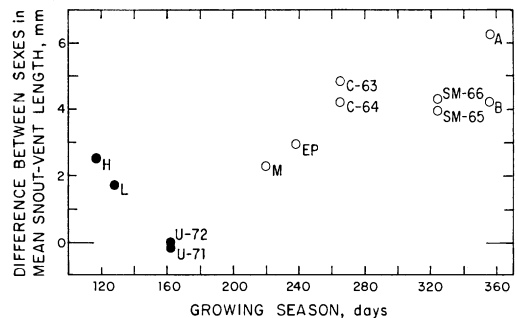


Fig. 7. Sexual dimorphism in snout-vent length of adult *Uta* plotted against growing season. Spots = northern areas; circles = southern areas.

TABLE 7. FREQUENCIES OF BROKEN REGENERATED TAILS OF ADULT ( $\geq 41$  MM) *Uta stansburiana* FROM 17 LOCALITIES.

Area	Years	Latitude	Males		Females		Combined	
			N	%	N	%	N	%
W	62	46° 50'	5	60.0	6	16.7	11	36.4
I	62	42° 36'	6	50.0	8	14.3	14	44.2
H	62	42° 25'	57	50.9	29	31.0	86	43.0
U2	70-72	40° 36'	134	50.0	108	34.2	242	43.0
L	64	40° 12'	28	39.3	36	36.2	64	37.5
G	64	38° 48'	11	72.7	18	38.9	29	51.7
V	64	37° 05'	19	42.1	9	66.6	28	50.0
P	64	36° 18'	5	40.0	7	14.3	12	25.0
S	64	35° 18'	10	70.0	23	69.5	33	69.7
M	63	35° 06'	55	40.0	56	51.8	111	45.9
T	63-64	34° 08'	8	62.5	2	50.0	10	60.0
R	63-64	33° 41'	22	68.2	22	68.2	44	68.2
SM	65-66	33° 26'	215	47.5	176	40.9	391	44.5
C	63	32° 57'	65	78.5	77	65.0	142	71.2
C	64	32° 57'	111	46.9	94	57.4	205	51.7
EP	70	31° 50'	19	36.9	17	35.3	36	36.2
B	69	29° 38'	11	63.6	14	86.7	25	76.0
A	69	28° 20'	17	76.5	21	47.6	38	60.5
North			260	49.6	214	34.5	474	42.8
South			538	55.6	509	53.1	1047	54.3
Total			798	53.6	723	47.5	1521	50.6

growing seasons have high survivorship but small size (Tinkle, 1967, 1969a).

*Latitudinal trends in sexual dimorphism.*—Tinkle (1969a) noted little sexual dimorphism in color pattern of utas from his northern area, but marked dimorphism in his southern population. Another, more easily quantified, measure for degree of sexual dimorphism is difference in body size between the sexes. Among our northern areas with adequate sample sizes, there is moderate dimorphism on two areas (Hart Mountain National Antelope Refuge, Oregon, and Lovelock, Nevada), while on a third (Grantsville, Utah) there is no significant difference between the sexes (Fig. 7, Table 6). On southern areas, degree of size dimorphism is positively correlated with growing season, inferring a premium on greater difference in size between the sexes on areas with long seasons favorable for activity. A similar pattern of increase in degree of aggressive behavior in males from north to south should occur (Tinkle, 1967). Where aggressive behavior is intense, selection might favor female phenotypes allowing immediate recognition of sex. In populations with

all males having larger body size and different color patterns from females, energy expenditure in defense of territories could be reduced through such facilitation of sex recognition.

#### BROKEN TAILS AND PREDATION

Broken tails increase significantly from north to south in the teiid, *Cnemidophorus tigris*, directly correlated with an increase in number of potential predators (Tables 5 and 6 of Pianka, 1970). *Uta stansburiana* shows a similar pattern over the same geographic area (Table 7). In combined samples, northern utas have a broken tail frequency 11.5% lower than southern utas. This difference would be even greater if standardized to an equal age basis, since northern utas live longer than southern ones. By sex, there is only a slight difference between northern and southern males (6%), but southern females have 18.6% more broken tails than northern ones, accounting for most of the difference between combined samples. Higher frequencies of broken tails in the south are presumably the result of higher frequency of encounter with a higher density and diversity of

TABLE 8. FREQUENCIES OF BROKEN REGENERATED TAILS BY SIZE CLASS IN TWO SOUTHERN AND ONE NORTHERN POPULATION OF *Uta stansburiana*.

Size class (mm)	SOUTHERN AREAS						NORTHERN AREA			TOTALS		
	(Casa Grande, Arizona)			(South Mountain, Arizona)			(Grantsville, Utah)			(All Three Areas Combined)		
	N	No. Broken	% Broken	N	No. Broken	% Broken	N	No. Broken	% Broken	N	No. Broken	% Broken
21-30	27	5	18.5	257	46	17.9	8	1	12.5	292	52	17.8
31-40	141	40	28.4	134	40	29.8	45	4	8.9	320	84	26.2
(Females)												
41-50	95	60	63.2	143	57	39.8	79	23	29.2	317	140	44.2
51-	76	44	57.9	33	15	45.5	29	14	48.3	138	73	52.9
(Males)												
41-50	15	4	26.6	79	29	36.7	112	56	50.0	206	89	43.2
51-	161	99	61.5	136	73	53.6	22	11	50.0	319	183	57.4

predators. Tinkle (1967), however, found that Texas utas were much more aggressive than Colorado lizards. This suggests that at least some breakage in southern lizards results from intraspecific aggressive encounters between members of the same sex. Moreover, greater aggressiveness could increase the frequency of exposure to predators.

Three areas with large sample sizes were selected for analysis of broken tail frequency by size class to detect differences between northern and southern areas (Table 8). The primary difference between the two southern areas and the northern area is an almost twofold increase in frequency of broken tails of 21-40 mm lizards from north to south ( $\chi^2 = 5.16$ ,  $P < .05$ ). By the above reasoning, this difference could be the direct result of the southward increase in number of predators, and none should be attributable to intraspecific aggression since all are immature animals. Alternatively, the difference might indicate greater intraspecific aggressiveness between juveniles in the south, since aggressive behavior could conceivably develop before attainment of maturity (Tinkle, 1967). Frequencies for the northern (Grantsville, Utah) and southern (South Mountain, Arizona) adult males and females are generally similar (males with higher frequencies than females), but in another nearby southern area (Casa Grande, Arizona), females exhibit tail-break frequencies similar to males. Factors leading to the difference in frequencies in adult females between these two southern areas are unknown.

#### REPRODUCTION

*Testicular cycle.*—There is little difference in the gross testicular cycle of utas from different localities. Testes regress about a month earlier at Phoenix, Arizona than in northern Utah or southern New Mexico (Fig. 8). Perhaps more activity can take place in the winter months in Arizona than at the other localities, favoring an earlier termination of breeding. Breeding season length is apparently about 3-4 months at all three localities. Testicular cycles in Texas (Tinkle, 1961) and southern Arizona (Asplund and Lowe, 1964) are most similar to our results for Utah and southern New Mexico. Under a rather wide latitudinal range with different growing season lengths and meteorological characteristics at each of five localities, variation in the testicular cycle is minimal, as it is in *Cnemidophorus tigris* from three of the same locations (Parker, 1973b). Thus, testicular cycle is a relatively fixed life history parameter, not influenced as much by normal climatic variations as clutch size (below).

*Seasonal trends in clutch size.*—Utas characteristically lay smaller clutches as the season progresses (Tinkle, 1967; Hoddenbach and Turner, 1968), and our data constitute no exception (Fig. 9). Females from South Mountain, Arizona, and Stansbury Island, Utah (1963) showed marked reductions in clutch size late in the season, while those from Grantsville, Utah (1971) and southern New Mexico exhibited only slight decreases. Decreases seem less marked in northern populations laying only one

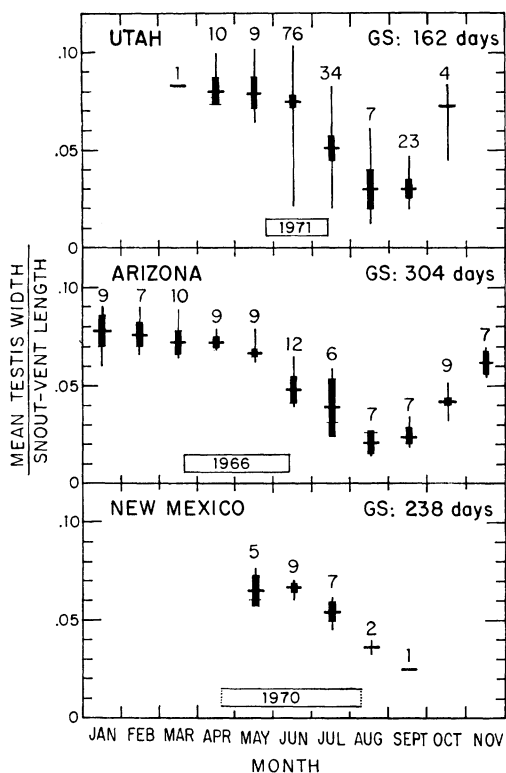


Fig. 8. Changes in testicular size by month for male *Uta stansburiana* from one northern (U2) and two southern areas (SM and EP). Horizontal lines = mean; vertical lines = range; vertical bars = 95% confidence limits on means; horizontal bars = period of oviducal eggs for year indicated; numbers = sample size.

clutch (Grantsville, Utah, 1971) than in southern populations with multiple clutches or in northern ones laying two clutches (Stansbury Island, Utah, 1963). Reduction of clutch size late in the breeding season may characterize some early-maturing lizards (Tinkle, 1969b), since *Sceloporus undulatus* (Tinkle and Ballinger, 1972), *Sceloporus olivaceus* (Blair, 1960), *Urosaurus ornatus* (Martin, 1973; Parker, 1973a), *Cnemidophorus tigris* (Parker, 1972b) and others also exhibit reduced clutch size late in the season. Presumably reduced late season clutches may be influenced by several factors, including progressive maturation of small yearling females resulting in a smaller average size of gravid females late in the season, and also decreased energy stores for large clutches by older females laying successive clutches. Food availability might decrease as the season progresses as well (Pianka and Parker, 1975).

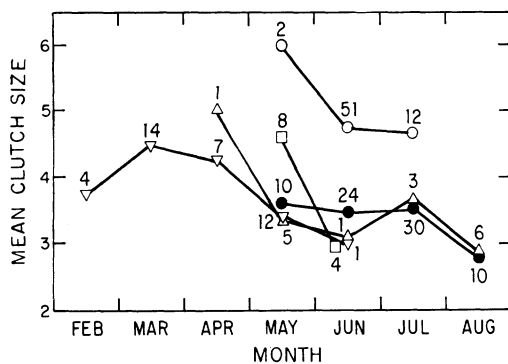


Fig. 9. Monthly changes in mean clutch size for *Uta stansburiana* from one northern and two southern areas. Spots = Utah 1963 (U1); circles = Utah 1971 (U2); squares = Utah 1972 (U2); triangles = New Mexico 1970 (EP); inverted triangles = Arizona 1966 (SM); numbers = sample sizes.

*Seasonal cycle in females.*—Monthly frequencies of gravid females are shown for eight different years at four different areas in Fig. 10, with areas arranged in decreasing order of length of growing season from bottom to top. Oviducal eggs occur over short periods (3–4 months) at both Grantsville, Utah, and South Mountain, Arizona, and over longer periods (5–6 months) in the areas with intermediate growing season lengths (Southern New Mexico and Casa Grande, Arizona). Fitch (1970), however, found gravid females from Baja California (long growing season) over eight months (Jan.–Aug.). In the continental United States, most egg laying occurs between May and early August in northern areas, and in southern areas with intermediate growing seasons. In other southern areas, oviducal eggs occur earlier in the year, and most egg laying takes place between March and early June (South Mountain, Arizona).

Number of clutches per year is generally 1–2 in northern areas (Stansbury Island, Utah, 1963; Christiansen, 1965), and two or more in southern areas. As many as five clutches per year have been reported, but number of clutches can vary widely from year to year at the same locality (Turner et al., 1970). Our data suggest that more clutches are laid in southern areas than northern ones in some years (EP-70, C-64), but not in others (C-63, SM-65, SM-66). Occurrence of oviducal eggs suggests that the northern areas U1 and U2 normally have 1–2 clutches per year, while the three southern areas (EP, C, and SM) vary between 2–4 clutches per year (Fig. 10). On area U2 (Grantsville, Utah) in 1971, oviducal eggs occurred over a 49-day

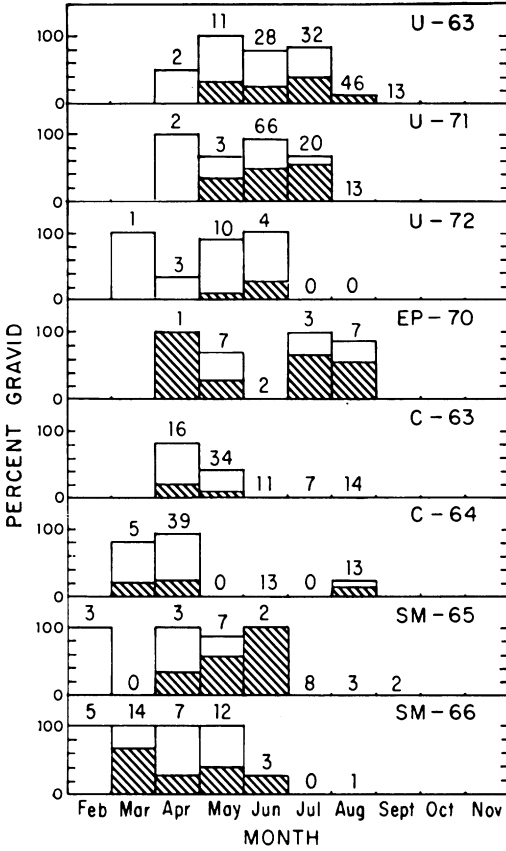


Fig. 10. Monthly frequencies of gravid female *Uta stansburiana* from two northern (U1-63, U2-71 and 72) and three southern study areas (EP, C and SM). Cross hatching = oviducal clutches; numbers = sample sizes.

span (24 May–12 July) and hatchlings emerged in a period of less than 30 days (August), suggesting that most females laid only one clutch. On area SM (South Mountain, Arizona) in 1966, a 98-day period of females with oviducal eggs was noted (18 March–24 June), and a maximum of 3 clutches was produced, based on the numbers of emerging hatchlings (Parker, 1974).

*Factors influencing clutch size.*—Tinkle (1967) and Fitch (1970) indicate that northern utas have smaller clutches than southern ones. Tinkle further reasoned that the difference exists because northern females mature at smaller sizes and thereby must produce smaller clutches. Hoddenbach and Turner (1968) demonstrated that clutch size of Nevada utas varies from year to year and within breeding seasons of some years, being higher after good growth of

winter annuals which presumably increases their food supply. Tinkle et al. (1970) analyzed clutch size in populations from six states and found significant correlations between clutch size and body size in 14 of 24 samples. Using these publications as guidelines, we analyzed 384 clutches by partial correlation and stepwise multiple regression, using the following variables as ones likely to influence clutch size:

- 1) SVL
- 2) Latitude
- 3) Length of growing season
- 4) Precipitation (as an indicator of primary productivity)
  - a) Pptn-6: total during 6 months prior to month of collection
  - b) Pptn-12: total during 12 months prior to month of collection
  - c) Pptn-18: total during 18 months prior to month of collection
  - d) Ltm: long-term average annual precipitation
- 5) Date of collection

Difficulties in analysis arise primarily from small samples at some localities and in precipitation data being taken from weather stations somewhat too distant to reflect conditions accurately at the actual spots where lizards were collected. Our initial analysis included all gravid females and showed that the factor influencing clutch size most strongly was the total precipitation during the 12-month period prior to the month of collection. Northern and southern areas were then analyzed separately, with results from multiple regression as shown in Table 9. Partial correlation analysis shows that clutch size in northern populations is significantly correlated with Pptn-6 ( $r = .626$ ,  $P < .05$ ), followed by Ltm ( $r = .471$ ) and SVL ( $r = .457$ ). The best correlation for southern populations is a negative one with date of collection ( $r = -.497$ ). Multiple regression analysis shows the same major influences on clutch size as does partial correlation. Pptn-6 reduced variance in clutch size by 38.8% in northern populations, followed by Pptn-12 and SVL. Date accounts for 21.6% of the variance in clutch size in southern populations, followed by SVL and latitude.

The influence of SVL on clutch size seems to fit the following pattern. The smallest females (37–44 mm) all lay small clutches of 1–4 eggs and the largest ones (52–56 mm) lay only clutches of 3–7 eggs. Intermediate-sized females have widely variable clutches between

TABLE 9. SEPARATE STEPWISE MULTIPLE REGRESSIONS FOR CLUTCH SIZE IN NORTHERN AND SOUTHERN POPULATIONS OF *Uta stansburiana*.

Variable	North (N = 201)				South (N = 166)			
	ID	r	r <sup>2</sup>	% variance	ID	r	r <sup>2</sup>	% variance
First	Pptn-6	.623	.388	38.78	Date	.465	.216	21.60
Second	Pptn-12	.669	.448	5.97	Lat.	.540	.292	7.57
Third	SVL	.703	.494	4.68	SVL	.620	.385	9.30
Fourth	Date	.712	.507	1.22	Pptn-12	.625	.391	.60
All Five								
Others		.732	.536	2.90		.635	.403	1.20
TOTAL				53.62				40.26

1 and 7 eggs, depending primarily on date and/or recent precipitation. Regressions of clutch size on SVL in populations with reasonably large samples produced significant correlations in only three of nine cases (Table 10). Samples from other years for both these populations are not significantly correlated. Results for the three Utah collections [plus Tinkle et al. (1970) data from the same locality] show significant correlations between clutch size and SVL in the years with above average recent precipitation (1967, 1971 and 1972), but no correlation in the one year with below average recent precipitation (1963).

A further example of the effect of recent precipitation on clutch size concerns our areas with clutch records for two different years (Table 10, Fig. 10). On areas C, M and U2, clutch size changes were in all cases proportional to recent precipitation. At Casa Grande, Arizona, however, the mean size of gravid females also increased, as well as the proportion of early clutches in the sample. In contrast, on the Utah areas between 1963 and 1971, there was no change in female size or season of collection, yet clutch size increased by 1.4 eggs. This increase correlates neatly with a massive increase in recent precipitation. Moreover, the other two Utah collections fall into place between the 1963 and 1971 samples for both mean clutch size and recent precipitation. The significance of date in southern populations is undoubtedly the result of multiple clutches, which either do not occur or are less frequent (maximum of two) in northern populations. Seasonal trends on various areas only partially substantiate the importance of date (above).

*Reproductive effort and expenditure per progeny.*—Reproductive effort (RE) per clutch for each study area (N = 125 oviducal clutches) was

compared with three other variables: clutch size, SVL and growing season. On northern areas, there is a weak positive correlation between clutch size and RE ( $r = 0.10, P > .05$ ), but for southern populations the correlation is somewhat stronger ( $r = 0.48, P < .05$ ) (Fig. 11). RE per clutch is only loosely correlated with average SVL in both northern and southern populations. Relatively small females can have high RE's (areas H, W and EP). The most revealing correlation is between RE and growing season (Fig. 12), showing an apparent depression of RE at both extremes of the species range. This depression presumably results from environmental extremes: in the north (N, L, G), perhaps temperature and/or length of growing season, and in the far south (A, B), perhaps aridity and/or competition. At these extremes, female utas apparently do not put as much into each act of reproduction as they do in climatically more favorable environments in the center of their geographic range, which results

TABLE 10. REGRESSIONS OF CLUTCH SIZE ON SNOUT-VENT LENGTH IN VARIOUS *Uta* POPULATIONS WITH REASONABLY LARGE SAMPLES.

Area-Year	N	Mean SVL	Mean Clutch	b	a	r
H-62	27	43.0	2.85	.050	0.723	0.19
U1-63	74	48.5	3.41	.060	0.52	0.17
U2-67*	31	46.2	4.39	.288	-8.917	0.713
U2-71	65	48.9	4.82	.228	-6.34	0.53
U2-72	14	49.3	4.21	.086	-0.197	0.62
SM-65	13	51.1	4.00	.308	-1.17	0.70
SM-66	37	47.4	4.00	.055	1.38	0.12
C-63	27	50.0	3.78	.078	-1.42	0.16
C-64	44	51.1	4.48	.053	1.73	0.14
EP-70	16	46.9	3.31	.085	-6.82	0.21

\* From Tinkle et al. (1970).

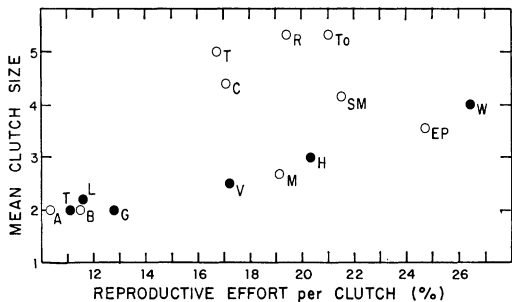


Fig. 11. Mean clutch size of *Uta stansburiana* plotted against average reproductive effort (total wet weight of oviducal eggs over total wet weight of female). Spots = northern areas; circles = southern areas.

in depression of both RE per clutch and clutch size. Further, this decrease in RE is not particularly due to reduction of body size since these five areas have average female snout-vent lengths up to 48 mm. Presumably, fecundity on the two southern areas with low RE is augmented by multiple clutches, which may partially compensate for the low RE per clutch. This higher fecundity is probably a direct result of a biotically less favorable environment (more competitors and predators than in the north). In contrast to our data for *Uta*, Tinkle and Ballinger (1972) found relatively minor differences in RE per clutch among two northern and two southern populations of the iguanid *Sceloporus undulatus* (only 23-27% versus 9.7-30.5% in *Uta*).

Expenditure per progeny, or EPP, was compared with mean clutch size and growing season (Fig. 13, 14). Northern lizards have consistently high EPP, regardless of clutch size, whereas southern utas show a significant negative correlation ( $r = -.73, P < .05$ ) between

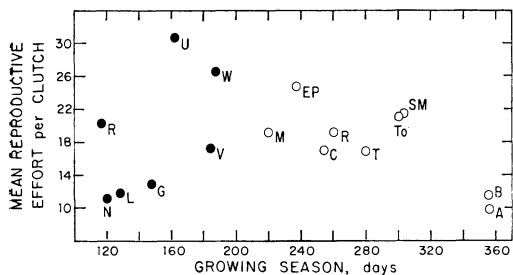


Fig. 12. Mean reproductive effort per clutch plotted against growing season. Spots = northern areas; circles = southern areas. The inverse correlation for southern areas is statistically significant ( $r = -.71, P < .05$ ).

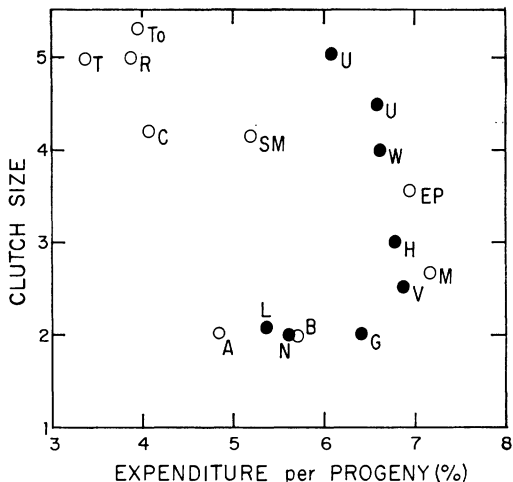


Fig. 13. Mean clutch size of *Uta stansburiana* plotted against the mean expenditure per progeny (weight of one oviducal egg over the total wet weight of female). Spots = northern areas; circles = southern areas.

clutch size and EPP (i.e., larger clutches have smaller eggs). This again contrasts with *Sceloporus undulatus* which shows only slightly lower EPP in southern populations (Tinkle and Ballinger, 1972).

Along and  $r$ - $K$  selection continuum (Pianka, 1972), *Uta stansburiana* is relatively  $r$ -selected as a lizard species, producing more than one relatively large clutch annually throughout most of its range. Our data indicate an  $r$ - $K$  selection continuum from south to north within the species. Southern populations, in general, produce numerous clutches of relatively small eggs, expending less energy on each individual progeny and produce more of them. In contrast, northern populations all produce few clutches of relatively large eggs, expend more energy on each individual progeny and produce fewer of them in one year. The number

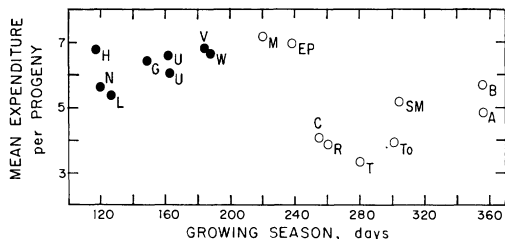


Fig. 14. Mean expenditure per progeny of *Uta stansburiana* plotted against growing season. Spots = northern areas; circles = southern areas.



of eggs per clutch is the result of a complex of factors as discussed above. Comparison of expenditure per progeny and growing season again shows that all northern areas and two southern areas with long growing seasons have high expenditures per progeny (Fig. 14). Among remaining southern areas, expenditure per progeny and growing season are positively correlated ( $r = .76$ ,  $P < .05$ ). This suggests that the reduced clutch size of the extreme southernmost populations (like those of northern populations) is partially due to an increased expenditure per progeny. Within southernmost populations, there may thus be another continuum of  $r$  to  $K$  selection, but in this case from north to south.

Davis and Verbeek (1972) studied *Uta* at its western range limit in California, and found density-independent factors (greater sky cover and lower temperatures in late summer) to be the chief causes for the absence of the species. More detailed study of these and other extreme populations should prove enlightening on major factors which influence reptilian range boundaries in temperate regions. Larger collections of gravid females from many populations at the northern and southern extremes of the range, correlated with more population studies, should help to clarify geographic changes in reproductive effort further. Also, direct correlations between egg size, hatchling size, and increased survivorship need to be established.

#### CONCLUSIONS

While many of our conclusions must remain tentative, numerous ecological differences do exist between northern and southern populations of *Uta stansburiana*. Southern populations have more predators, shorter daily but longer seasonal periods of activity, more competitors, greater sexual size dimorphism, and they mature at larger sizes. Diets of northern and southern populations are generally similar, except that southern utas eat more termites. Clutch size is correlated with recent precipitation (past 6 months) in the north, and with both date of collection and snout-vent length in the south. Southern populations generally produce numerous clutches of small eggs, expend little energy on each individual progeny but produce many of them. Northern populations produce few clutches of large eggs, expend more energy on each individual progeny, and produce fewer offspring per year. As in the teiid, *Cnemidophorus tigris* (Pianka, 1970), the ecological challenges facing *Uta* in the north

appear to be primarily climatic ones, whereas in the south biotic interactions (particularly predation and competition) may assume relatively greater importance.

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