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SCELOPORUS UNDULATUS: COMPARATIVE LIFE HISTORY AND REGULATION OF A KANSAS POPULATION[1]

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Abstract. The demography of a small, isolated population of the lizard *Sceloporus undulatus garmani* from eastern Kansas, USA was studied for 5 yr. Growth rates were relatively rapid; age of maturity, relatively low; clutch size was small and decreased in successive clutches of the same females; juvenile survival, while low, was high for the species; adult survival was relatively low. The population size was the most variable yet studied. Winter-spring mortality rates, probably due to predation, were constant regardless of density, but density-dependent mortality operated in at least 1 yr during this period. Summer-fall recruitment was density dependent, probably due to predation on egg-laying females, but flooding and possible temperature-dependent predator susceptibility resulted in instability of the population size. The population is probably below its resource limits most of the time. The comparative demography of this and eight other populations of *S. undulatus* reported in the literature was summarized. There are three ecological regions to which this species has adapted: eastern woodland, grasslands, and canyonlands. There are both regional and latitudinal differences in suites of correlated traits, but comparative data on ecological pressures are not sufficient to support any single current theory of how these different populations are adapted.

Key words: comparative demography; geographic variation; life history; population regulation; Sceloporus undulatus.

INTRODUCTION

In the last decade, descriptions of demographic patterns of iguanid lizards have increased dramatically. Probably the species best studied from the point of view of geographic variation of life history characteristics is *Sceloporus undulatus* (Crenshaw 1955, Tinkle 1972, Tinkle and Ballinger 1972, Vinegar 1975). These variations are thought to be adaptations to different environmental pressures; but data on the role of resource availability, predators, and climate in the regulation of any of the populations are nonexistent (Fretwell 1972). In 1971 a demographic study was begun and continued with varying intensity through 1976 on a small isolated population of *Sceloporus undulatus* in eastern Kansas. The purposes of this paper are: (1) to summarize the basic demography and reproduction of the Kansas population, (2) to discuss possible factors regulating the population, and (3) to compare the life history patterns of this population with those studied by others and summarize geographic and regional trends of life history variation in this species. While considerable basic demographic data have accumulated on this species in other parts of its range, a synthetic comparison of all populations is lacking.

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MATERIALS AND METHODS

In the spring of 1971, an isolated population of the prairie swift *Sceloporus undulatus garmani* was located in eastern Kansas on the south shore of the Kansas River in Pottawattomie County, Kansas, ≈1.5 km south of the town of Belvue. While the prairie swift is abundant in sandy river bottoms in central and western Kansas, it is virtually absent from eastern Kansas except for a few isolated localities. The present population inhabits ≈ .3 ha of sandy bottom, and it surrounds a 1.6-ha pond located < 15 m from the river. Trees < 7 m (*Populus, Salix, Morus*) are scattered over the area, but most of the ground is not shaded; and the dominant vegetation consists of grasses and annuals such as *Sporobolus, Festuca, Bromus, Hoideum, Sattarius, Melanotus,* and *Solidago*. The lizards are concentrated in areas containing moderately sparse grasses and annuals and either cottonwoods (*Populus*) nearby or broken terrain such as a sand bank or gully. The only other common lizard species in the area is *Cnemidophorus sexlineatus* (see Ferguson and Bohlen 1972 for a list of other vertebrate species).

The population is completely isolated from any other conspecific population by numerous kilometers of unfavorable habitat. The age of the population is not known, but the entire expanse of favorable habitat was completely inundated by the great Kansas River flood

of 1951. So, it is likely that the population was either founded or severely bottlenecked at that time.

Data were gathered using standard mark and recapture techniques (see Tinkle 1967). Census of the population began in May 1971, and terminated in May 1976. Processing of individual lizards included capturing, measuring, and recording snout-vent lengths, clipping toes of lizards, weighing to the nearest 0.2 g with a Pesola field scale, recording toe-clip number for future identification of individuals, recording location, recording habitat, painting the tail base, and releasing at the place of capture. The area was searched systematically and repeatedly. On the first search, all lizards seen were captured and processed. On subsequent searches, all lizards lacking a paint mark were captured and processed while those with a paint mark were only tallied. After six to eight systematic searches, the proportion of "new" lizards was usually <10% and the census was considered complete. Then, population sizes were estimated using the Hayne index (Hayne 1949). Due to the high rate of hatching in the period from 23 July 1971 through 7 September 1971, and the low man power available during that time, that entire 47-d period was considered a single census. The first census in May 1971, and those beginning in late September 1971, were shorter and included roughly 10–14 d periods. The midpoints of census periods from October 1971 to May 1974, were about 1 October (posthatching period), 1 April (prebreeding period), 20 May (midbreeding period), 10 July (postbreeding period-prehatching period), 1 August (early hatching period), and 22 August (late hatching period). After this date census midpoints were 15 October 1974, 10 June 1975, 1 October 1975, and 30 May 1976. Data from these censuses allowed the calculation of growth and survival as well as density. A total of over 1100 lizards were marked on this area.

Local climatological data for some analyses were obtained from the United States Department of Commerce for Philip Billard Field in Topeka, Kansas. The Belvue study site was located about equidistant from Topeka to the east and Manhattan to the west. Climatological data (minimax air temperature, rainfall, estimated cloud cover) obtained on the study site in 1971 correlated more closely with the Department of Commerce data for Topeka than that for Manhattan. River levels were from Wamego, Kansas (≈ 8 km downstream from the site).

Reproductive data from female lizards were obtained by direct counts of eggs laid in outdoor enclosures by female lizards collected from a population of *S. undulatus garmani* in Reno County, Kansas. Due to the small and fragile nature of the Belvue population, lizards were not removed from that area.

Density dependence was analyzed after the manner of Fretwell (1972) as follows: Death rate of lizards was calculated by the formula

$$d = \frac{Nw(t) - Ns(t+1)}{Nw(t)},$$

where $Nw(t)$ = the number of lizards, mostly juveniles, alive at the end of the hatching season (October), $Ns(t+1)$ = the number of lizards alive at the midpoint of the following spring breeding season (May). Values for different years were then plotted as a function of $Nw(t)$. Birth rate (reproductive success) was calculated by the formula

$$b = \frac{Nw(t) - Ns(t)}{Ns(t)}$$

where $Ns(t)$ = number of lizards alive in spring; $Nw(t)$ = number of lizards alive the following fall. Values for each year were then plotted as a function of $Ns(t)$.

Density dependence was also analyzed by comparing the simultaneous growth rate and survival of juveniles on high- vs. low-density areas of the study area over 1-mo periods during the summer. The entire study area was subdivided into 24 quadrats. Those quadrats whose density was included in the upper half of the range of densities of all quadrats were considered high-density quadrats. Those whose density fell in the lower half were considered low-density quadrats. Thus the absolute criteria varied with each analysis.

Results and Discussion

Life history of the Kansas population

A summary of the major features of the life history of the population is presented below. A more detailed account is being prepared for publication elsewhere.

Hatchling growth and age of maturity in Kansas.—The hatching period of the Kansas population (15 July–15 September) is similar to that of the Colorado populations and is relatively short for the species (Tinkle 1972, Tinkle and Ballinger 1972). Hatchlings in Kansas grow as rapidly during the 1st 2 mo of life as in any populations previously reported (Tinkle and Ballinger 1972; 0.34, SE ± .01 mm/d, N = 111). As in most populations of this species, lizards mature by the age of 1 yr. Male courtship begins in April. Egg laying occurs from mid-May to mid-July. The reproductive success of late-hatching females maturing just in time to produce one late clutch the following July is possibly low. Males have an exceedingly high mortality during the months of April, May, and June (Ferguson and Bohlen 1972). At least one small female, observed intensively, first became gravid in early July. Her home range was located far from that of any male at that time, and she probably laid an infertile clutch.

Clutch size and frequency in Kansas.—Mean clutch size of 23 Reno County females that laid fertile eggs in captivity was 7.00 (SE ± 0.48) eggs, a relatively small value (Tinkle and Ballinger 1972). However, the mean snout-vent length of the females was also rela-

TABLE 1. Clutch size and egg size change of eleven females producing more than one clutch in outdoor enclosures near Manhattan, Kansas. Values are $\bar{x} \pm 1$ SE. $^*P < .05$; $^{**}P < .01$, ANOVA.

	Female body mass after laying eggs (g)	Mean egg mass per clutch (1×10^{-2} g)	Ratio of egg mass/female body mass	Clutch size
First clutch	5.48 ± .31	22.8 ± 1.6	.044 ± .005	8.7 ± 0.7
	NS	**	*	**
Second clutch	4.99 ± .22	28.9 ± 2.5	.059 ± .006	7.0 ± 0.4

tively small (mean 56.7 mm, SE ± 1.27) and ranged from 67 to 47 mm. As in all *S. undulatus* populations, there was a strong correlation between clutch size and body size ($y = .32x - 10.9$, $r = .86$, $P < .01$); and the clutch mass-body mass ratio was the highest reported for any population of this species ($\bar{x} = 0.28 \pm$ SE .01, $N = 23$). Mean clutch sizes of females decreased and egg sizes increased with successive clutches laid in outdoor enclosures (Table 1; see Ferguson and Bohlen 1978, for discussion of the significance of this). Clutch number varied from one to three. Most females (12) produced one clutch but 11 produced two or more. The largest females did not necessarily produce the most clutches.

Demography of Kansas lizards.—Survivorship was unusually variable and that of males generally less than that of females for a given time period. The mean survival from hatching to first breeding was among the highest recorded for the species and ranged from .09 to .24 ($\bar{x} = .18$) for males, from .25 to .30 ($\bar{x} = .27$) for females. Adult survivorship values, however, were lower than in most populations (Tinkle 1972, Tinkle and Ballinger 1972, Vinegar 1975). Survival of yearling adult males to a second breeding season ranged from .11 to .40 ($\bar{x} = .28$), that for females ranged from .18 to .42 ($\bar{x} = .30$). Only two lizards, one male and one female, survived to a third breeding season. The heaviest period of mortality for males was from March to May, that for females from May to July (Ferguson and Bohlen 1972).

TABLE 2. Life table for a Kansas population of *Sceloporus undulatus*. *mx* = number of female eggs produced by each female in each reproductive season; *lx* = survivorship from first age class to midpoint of age class over which *mx* is measured; R_0 = replacement rate per generation. See text for discussion of age class selection and table construction.

Age class (yr) (x)	Survivorship (lx)	Fecundity (mx)	Product ($lxmx$)
0	1.000	0	0
.25	.375	0	0
.83	.104	5.8	.603
1.83	.028	9.1	.255
2.83	.001	11.0	.011
			$R_0 = .869$

Female life tables were constructed in a fashion similar to that of Tinkle and Ballinger (1972) and Vinegar (1975) for other populations of *Sceloporus undulatus* (Table 2). In short, survivorship (lx) estimates were based on disappearance over those years of marked individuals hatched in 1971, 1972, and 1973. Fecundity (mx) estimates were indirect and based on size-fecundity relationships of samples of females taken from Reno County and evidence for a mean of two clutches per female. Age classes were: age 1-female eggs, age 2-age of hatching, ages 3, 4, and 5-midpoints of successive reproductive seasons. The replacement rate over the 5-yr period was less than one ($R_0 = .87$) which indicates that the population declined between 1971 and 1976. The critical period of decline was the severe crash in the summer of 1972 that followed a large increase in 1971. The breeding population (total numbers in May) steadily increased from 1972 through 1976. Numbers were: in 1971—77; 1972—102; 1973—33; 1974—36; 1975—43; 1976—47.

Regulation in the Belvue, Kansas population

While the ecological literature abounds with discussions of "population regulation" for a number of vertebrate and invertebrate species (Andrewartha and Birch 1954, Wynne-Edwards 1962, Lack 1966, Watson 1972), only a very few studies mention the subject for lizards (Tinkle 1967, Bustard 1970, Fretwell 1972). Details of the dynamics of population regulation are virtually unknown for reptiles including *Sceloporus undulatus*. Knowledge of the process is important for two reasons. First, the major ecological controversy of whether animal populations are regulated primarily in a density-dependent or primarily in a density-independent fashion can only be resolved by increased knowledge of the regulatory factors and how they operate for as many populations of as many species as possible. Second, knowledge of regulatory factors and their mode of influence has been proposed to be critical for testing various theories of life history evolution (Wilbur et al. 1974, Stearns 1976, 1977). We propose a tentative statement of the relative stability of the Belvue, Kansas population and will speculate on the methods of regulation.

The Belvue, Kansas population is a small, isolated population at the periphery of the range of the species. Many have predicted such populations to be relatively

TABLE 3. Variation of spring and fall densities of several lizard populations.

Species	Locality	Spring density: No. of seasons studied	Spring density: Mean no. lizards per ha (SD)	Spring density: Coefficient of variation ± 1 SE	Fall density: No. of seasons studied	Fall density: Mean density (SD)	Fall density: Coefficient of variation ± 1 SE	Authority
Sceloporus undulatus	Texas	3	2 (.3)	16.5 ± 6.9				Tinkle and Ballinger 1972
	Kansas (Belvue)	5	48 (22.3)	46.7 ± 17.6	4	112 (33.8)	30.2 ± 11.5	This study
	Kansas (Reno County)	3	46 (9.3)	20.2 ± 8.5				Bohlen 1976
	South Carolina	3	8 (2.1)	27.9 ± 12.1				Tinkle and Ballinger 1972
	Ohio	3	22 (3.1)	14.3 ± 5.8				Tinkle and Ballinger 1972
	Colorado	3	14 (.7)	5.2 ± 2.1				Tinkle and Ballinger 1972
	Utah	2	33 (1.3)	3.9 ± 2.0				Tinkle 1972
Sceloporus graciosus	Utah	3	208 (5.7)	2.7 ± 1.1				Tinkle 1973
Sceloporus olivaceous	Texas	5	52 (6.0)	11.6 ± 3.7	4	157 (29.8)	19.0 ± 6.9	Blair 1960
Uta stansburiana	Texas	4	36 (13.0)	35.7 ± 14.1	3	194 (39.8)	20.5 ± 8.7	Tinkle 1967
Crotaphytus collaris	Kansas	6	35 (13.8)	39.0 ± 12.8		66 (30.1)	45.7 ± 15.6	Fitch 1956

unstable (more unpredictably variable) compared to larger, more centrally located populations of a species and to be regulated more by density-independent than density-dependent factors (Ehrlich et al. 1972, Krebs 1972, pages 280–281). The Belvue population may conform to these two predictions (Table 3, Fig. 1). The coefficient of variation of spring density seemed to be greater for the Belvue population than for the larger, more centrally located population in Reno County, Kansas, and is the largest recorded for any lizard studied over a comparable period of time. Due to the small number of seasons used in the calculations, however, the standard errors are large and conclusions remain tentative. Furthermore, we can say little about the predictability of these variations over a longer time span.

The regulation of the population seems to be a complex interaction of density-dependent and density-independent factors. Density-independent factors possibly predominate, but conclusions based on a cursory examination of a year-to-year plot of population growth vs. density may be misleading. To dissect the situation further, it is convenient to divide the year into two seasons (Fig. 1). The winter-spring season includes only mortality. Mortality rate and late-fall density were used to plot the death rate (d) curve. The summer–fall season includes an interaction of birth and mortality. Birth rate is higher than death rate at this time; data on population increase and late-spring density were used to plot the birth rate (b) curve (Fretwell 1972).

Winter–spring mortality factors.—Mortality rate is constant and high throughout this period (d ranged from .73 to .78), regardless of beginning density (Fig. 1). Nevertheless, we cannot say that density-dependent factors are totally inoperative at this time. Thus, in the highest density year (October 1971 to May 1972), mortality rates of both males and females were significantly higher (χ^2 test, $P < .05$) on the more dense quadrats than on the less dense quadrats of the study area. Density-dependent mortality of males establishing breeding territories at the end of this time period was measured the same way and was highly significant in 1972 (χ^2 test, $P < .01$, see Ferguson and Bohlen 1972). Roughly a third of the mortality of the period resulted from the density-dependent mortality of males from March to May. A similar analysis for the year of lowest density (1972–1973) revealed no density dependence and that <10% of the mortality occurred from March to May. Despite the differences between years, the overall mortality was the same each year.

The factors operating during the winter–spring period remain obscure. Lizards spend most of this period hibernating in mammalian burrows (mostly *Peromyscus* and *Microtus*). Death due either to poor microclimatic environments or predation by the mammalian inhabitants could be important. Perhaps the mammals

do not seek out high-density lizard congregations but merely supplement their diet with lizards in the proportion that they enter the mammals' burrow system. A constant mortality rate from year to year would result. If the lizard density became high enough to make the mammals slightly more reliant on lizards as a food item and more likely to seek them out, the effect could become mildly density dependent without necessarily increasing overall mortality rate relative to other years.

The spring period of male territorial establishment is a period of high-energy demand. Despite this, we feel that the density-dependent mortality of males in 1972 was a result of emigration to unfavorable habitat off of the study area where they are subject to predation, rather than that of death due to starvation. Aggression was high. Males did not seem emaciated in spring of 1972. Unfortunately, masses were not systematically collected for males until summer of 1972.

Summer–fall mortality factors. There was a density-dependent trend in birth rate (b) across years which, upon initial analysis, was not significant ($y = 3.65 - .02x$, $r = -.30$, $P > .05$, Fig. 1). Despite the trend, birth rate (b) was highly variable during this period, and events during this period clearly contributed more to the population instability than those in winter and spring. It is convenient to divide these events into two subsets, hatchling production and hatchling survival.

1. Hatchling production.—The number of eggs produced per female was probably roughly the same from year to year. We do not feel that limited energy which would influence this variable was a significant contributor to the variation of b. Thus, regressions of mass on snout-vent length were compared between females in May 1972 (highest density) and females in May 1973 (lowest density). Palpation revealed that most females were gravid in May of both years. Then, female regressions of the same variables were compared for July of both years. Most females were postreproductive in July. No significant differences in regressions between the two years were found (Chow test, $P > .05$, Chow 1960). Thus, the females were comparably robust in each year, both before and after egg laying, and probably laid similar-sized clutches. Females can apportion energy somewhat differently. They can manufacture either fewer large or many smaller eggs (Table 1, Ferguson and Bohlen 1978); but, if they did, the difference in clutch size due to this mechanism would not be sufficient to account for the large difference in b between the two years. Without energy budget data or supplementary feeding experiments, we cannot prove that the females were not food limited to some degree. Resource availability could fluctuate directly with lizard density for some reason, and lizards in each year could have been under the same degree of food shortage. However, variation in egg production probably did not influence variations of b.

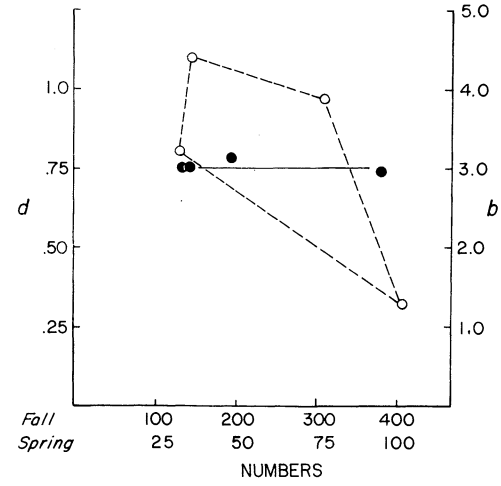

FIG. 1. Reproductive success (b) vs. spring numbers (○). Prereproductive survival (d) vs. fall numbers (●) for a population of *Sceloporus undulatus garmani* from Belvue, Kansas. Numbers are those on an entire study area.

An important density-dependent factor influenced female mortality during the egg-laying period from May to July. Female mortality was significantly density dependent across the area during this period in 1972, the highest density year (χ^2 test, $P < .01$; Ferguson and Bohlen 1972). The correlation between May numbers and mortality across years was high (Table 4, $r = .973$), but this value was not significant due to the small sample size ($N = 3$ yr). Because robustness was similar between years, females were not starving at a greater rate in 1972; and we feel that the density-dependent factor was predation, possibly by birds, which prevented a larger proportion of the females from laying their eggs in the higher density years.

If this factor alone were the most important factor affecting b, one would expect (1) the fairly similar numbers of females present on the area in each July to have produced roughly the same number of surviving young since they had similar "reproductive efforts," and (2) the fall densities to be more similar than they were. When b was recalculated using the July rather than the May female density, however, the 1972 value still appeared "abnormally" low (Table 4). What could have caused this low value? On 11 July 1972, while we were censusing the area, a torrential rainfall flooded the pond adjacent to the study area and inundated ≈25% of the study area. What is more important, the sandy ground became saturated over most of the study area for several days. Ground saturation could have caused considerable egg mortality and could have been the prime factor contributing to the very low recruitment that year. Certainly, sand that is "too wet" causes significant reduction in hatch-

TABLE 4. Female numbers, survival, reproduction, and temperature in three breeding seasons in a Kansas population.

	1971	1972	1973
Number of breeding females in May (*A*)	40	67	21
Number of postbreeding females in July (*B*)	25	21	15
B/*A* survival through breeding season	.63	.31	.71
Birth rate (*b*) based on female numbers at end of egg-laying season (July)	12.7	4.04	12.3†, 7.3*
Mean maximum temperature (°C) in May and June	26.9	27.3	26.6

† Estimated based on population size before the October flood.
* Based on postflood population size.

ing success in constant temperature incubators in the laboratory (Ferguson, *personal observation*).

2. Hatchling survival.—Yet another factor contributed to a variable recruitment during this study. There was considerable variation between years of juvenile survival during August and September. This variation seemed correlated more with temperature ($r = .978$) than numbers ($r = .84$, Table 5), although small sample size precluded statistical significance of the high correlation. It seems unlikely that a temperature range of only 2°C, which in none of the years included low temperatures near freezing, could kill directly exposed lizards. Alternatively, temperature could have influenced other pressures including either the intensity of predation or availability of resources.

We believe that the temperature affected overall predation. Thus, survival rate was significantly density dependent across the area only in 1972, when overall density and survival was lowest (Table 6). Growth rates, however, were significantly density dependent only in 1971 when density and survival were the highest. Variance of growth rate also was significantly higher in 1971 than in 1972. A density-dependent and variable growth rate in 1971 suggests that resource competition was more intense that year; but this did not result in either depressed overall survival or growth rate, both of which were the highest recorded in any year (Table 5). Perhaps lizards, unable to reach their optimal temperature in 1972, were slower and more susceptible to predation in that year. Also, one predator was conspicuously present in the daytime in 1972 but not in other years, the toad *Bufo woodhousei*. Tethered lizards offered to medium-sized toads in the field were readily devoured. In short, while egg mortality due to flooding had set the stage for the "crash of 1972," the heightened rate of predation in that cool year possibly was responsible for magnifying the effect. Predation pressure was more related to density in the egg-laying season because temperature was more constant (Table 4).

Flooding dramatically depressed the recovery of the population in October 1973. With the fall census nearly completed, the Kansas River inundated ≈75% of the study area. By exhaustive postflood census, we determined that 44% of lizards marked prior to the flood were lost. Thus, *b* calculated that year from the postflood juvenile crop was lower than that expected from the spring female population (Fig. 1). A recalculation of *b* in 1973 using the estimated preflood rather than postflood fall population resulted in a highly significant negative correlation between May female population and *b* ($r = -.994$, $P < .01$). Perusal of the records of daily river stages since the great flood of 1951, which remained up to 3.4 m over flood stage for 14 d, revealed that flood stages comparable to that of October 1973, occurred in the midsummers of 1960 and 1961.

TABLE 5. Juvenile growth, survival, numbers, and temperature in a Kansas population of *Sceloporus undulatus* in August and September.

	Juvenile survivorship in August and September					
Year	Number marked in early August	Number recaptured in late September	Proportion recaptured	Juvenile growth (mm/d) in August and September $\bar{x} \pm 1$ SE (*N*)	Estimated number of juveniles on area in early September	Mean maximum August temperature (°C)
1971	214	101	.47	.344 ± .01 (111)	357	31.7
1972	63	17	.27	.327 ± .01 (18)	72	29.7
1973	31	11	.35	.335 ± .01 (15)	210	30.9

TABLE 6. Growth and survival of juvenile *Sceloporus undulatus* in Kansas in low- and high-density sectors of the study area. $*P < .05$, t test or chi-squared test. See text for explanation of criteria for high- and low-density quadrats. Growth was significantly lower on high-density sectors in 1971. A significantly higher proportion of hatchlings survived on low-density sectors in 1972.

	Growth (mm) of hatchlings marked in late August $\bar{x} \pm$ SE (N)	Survival of hatchlings marked in late August		
		Number marked	Number recaptured	Proportion
1971				
High density 13 most dense sectors ≥12 lizards	.31 ± .01 (43) *	127	87	.69
Low density 11 least dense sectors <12 lizards	.35 ± .01 (32)	109	74	.68
1972				
High density 6 most dense sectors ≥3 lizards	.33 ± .01 (9)	37	14	.38 *
Low density 14 least dense sectors <3 lizards	.32 ± .01 (13)	19	13	.68

* Asterisks separate values which differ significantly from each other.

The flood of July 1972, was local and was not reflected by a rise in the river level. Thus, significant flooding effects may be even more frequent than every 10 yr.

To summarize, regulation in summer and fall involves density-dependent mortality, probably by predators, on egg-laying females. However, stability of population size is prevented by density-independent effects of flooding and by variable predation rate due to variable temperatures. Over the whole year, density-independent factors seem to predominate in the regular Kansas population. Also, population seems to be below the resource limits of the environment most of the time. Thus, the only time that resource competition seemed to be occurring (late summer, 1972) overall survival and growth rates were high (Table 5 and 6).

Horn (1968) presented several models of hypothetical populations which differed in their sensitivity to either density-dependent or density-independent factors. Several of his predictions require comment based on our study. First, he pointed out that both types of factors can interact, which is certainly the case in the Kansas population. Second, he pointed out that density-dependent factors may not necessarily stabilize the population if the sensitivity to the factor varies. Our hypothesis of the interaction of temperature and predation rates is an example of this. Conversely, density-independent factors such as those presumably operating during the winter in the Kansas population can be very constant and do not always contribute to instability. Third, Horn implied that populations regulated primarily by density-dependent factors should be closer to the environmental resource limits than those regulated by density-independent factors. This will only be true if the density-dependent factor is resource limitation. While the Kansas population may be subject more to density-independent than density-dependent regulation and seems to be below the resource limits, density-dependent predation, which might predominate in more flood-free portions of the range of *S. undulatus garmani,* also would keep the population below the environmental resource limits.

Geographic variation of life history in Sceloporus undulatus

This study and those by Tinkle (1972), Tinkle and Ballinger (1972), Vinegar (1975), and others have increased to at least ten the number of populations of *Sceloporus undulatus* whose life histories have been studied. Comparison of several life history characters (Table 7) reveals certain latitudinal and longitudinal trends of geographic variation. In addition to the comparative statements in the previous sections, we have chosen to summarize the latitudinal and longitudinal trends for each trait separately and then to discuss correlations between those trends.

Sceloporus undulatus inhabits three major habitat types, woodland or forest edge in the eastern United States, prairie or desert grassland in the central and much of the southwestern United States, and rocky plateau or canyonland in the mountainous regions of the western United States east of California and Nevada. In looking for latitudinal trends, it seems logical to divide the populations into those categories to prevent adaptational differences to their different habitats from obscuring any trends. Thus, for comparison, the populations from Ohio and Missouri were classified as northern eastern-woodland forms and those from South Carolina and Georgia were classified as southern eastern-woodland forms. The population from Kansas was considered a northern grassland form; those from Texas and Lordsburg, New Mexico, as southern grassland or desert grassland forms. The populations from Colorado and Utah were considered northern canyonland forms, that from Pinos Altos, New Mexico, a southern canyonland form. For each

TABLE 7. Comparison of life history traits of ten different populations of *Sceloporus undulatus*; ... means data not available.

Population	Texas	Lordsburg, New Mexico	Kansas	South Carolina	Georgia	Pinos Altos, New Mexico	Ohio	Missouri	Colorado	Utah
Minimum SVL* (mm) adult females	47	54	47	55	52	53	66	...	58	58
Mean SVL* (mm) adult females	57	68	57	63	62	63	75	...	70	69
Mean clutch size	9.5	9.9	7.0	7.4	7.6	7.2	11.8	11.3	7.9	6.3
Mean egg mass (g)	.22	.24	.26	.33	...	.29	.35	.38	.42	.36
Egg mass/body mass	.029	.022	.044	.033	...	.032	.021	...	.029	...
Number of clutches per year	3	4	2	3	3	2–3	2	2	2	3
Clutch mass/female mass	.27	.21	.28	.23	...	.22	.25	.28	.23	.21
Age at first breeding	1	1	1	1	1	1 yr-50% 2 yr-100%	2	...	2	1 yr-10% 2 yr-90%
Survivorship to age of first breeding	.06	.03	.10	.11	...	.02	.03	...	.11	.05
Average adult annual survivorship	.11	.20	.27	.49	.07	.34	.44	...	.37	.48
Mean number per hectare	2	10	48	8	...	35	22	...	14	33
Authority	Tinkle and Ballinger (1972)	Vinegar (1975)	This study	Tinkle and Ballinger (1972)	Crenshaw (1955)	Vinegar (1975)	Tinkle and Ballinger (1972)	Tinkle (1972)	Tinkle and Ballinger (1972)	Tinkle (1972)

* SVL = snout-vent length.

of the three regions, the traits in Table 7 were perused to detect latitudinal differences, then regional differences were observed.

Body size.—There are both latitudinal and regional differences in body size. In the eastern woodland and canyonlands, mature females are larger in northern populations. In the eastern portions of the grassland region, females are similar sized in both the north and south; but, in the more western desert grassland population (Lordsburg, New Mexico), females are larger. While eastern-woodland and canyonland females are similar sized, prairie *S. undulatus* females are the smallest.

Clutch size.—Clutch size and clutch size-body size relationships show no consistent overall latitudinal trends or regional differences. In the eastern woodland, the larger northern females had more eggs per clutch; but there was no significant difference in clutch size-body size regressions (Tinkle and Ballinger 1972). In the grassland and desert grassland region, the northern population had a smaller size specific clutch size. In the canyonlands, the northern populations differed from each other in clutch size-body size regressions and from the southern population, but there was no obvious north-south trend.

Mean egg mass.—There are both latitudinal and regional trends in egg mass. In the grassland and canyonland regions, the northern populations had the largest eggs. In the eastern-woodland region, the northern populations also had larger eggs; but north-south differences were small. The eastern-woodland and canyonland lizards were similar in having large eggs while the grassland and desert lizards had small eggs. These trends disappeared when egg mass was corrected for body size. There was variation with the Kansas lizards having the highest ratio.

Clutch frequency.—There is a latitudinal trend in clutch frequency but no regional differences. In the eastern-woodland and grassland populations, the northern populations had the fewest clutches of eggs. In the canyonland lizards, north-south trends were not clear-cut.

Clutch mass-female mass ratios.—There is a slight regional difference in this trait, but the variance in this feature is fairly low. The two highest values were for grassland forms.

Age of maturity.—There are both latitudinal and regional differences in age of maturity. In the eastern-woodland and canyonland lizards, the northern populations have delayed maturity relative to southern

TABLE 8. Rank and rank totals for five correlated parameters for several populations of *Sceloporus undulatus*. Tied values were given the average value of the two or more tied ranks.

Population	Rank body size	Rank age of maturing	Rank annual adult survival	Rank egg size	Rank female mass/ clutch mass	Total of ranks	Rank of rank totals
Texas	7.5	6.5	8	8	7	37	1
Kansas	7.5	6.5	6	6	8	34	2
Lordsburg, New Mexico	4	6.5	7	7	1.5	26	3
South Carolina-Georgia	5.5	6.5	5*	4	4.5	25.5	4
Pinos Altos, New Mexico	5.5	4	4	5	3	21.5	5
Ohio	1	1.5	2	3	6	13.5	6
Colorado	2	1.5	3	1	4.5	12	7
Utah	3	3	1	2	1.5	10.5	8

* The rather disparate values of this parameter from South Carolina and Georgia were averaged for this analysis.

populations. Grassland and desert grassland lizards mature the earliest, the canyonland lizards the latest.

Prebreeding survival.—There is a latitudinal trend but no regional difference in prebreeding survival. In the grassland and canyonland lizards, prebreeding survival is higher in the north.

Annual adult survival.—There is a slight latitudinal trend and a regional difference in average annual adult survival. Canyonland and grassland forms survive slightly better in the north. The grassland and desert grassland populations have the lowest annual adult survival.

Density.—In the grassland and desert grassland regions and in the eastern-woodland region, lizards tend to be more dense in the north. There seems to be no latitudinal trend in canyonland lizards nor do there seem to be any regional differences in density.

Stability.—Only six populations have been studied three or more years (Table 3). For these populations coefficients of variation of population density give some measure of instability. There are no clear-cut regional or latitudinal trends based on this sample.

Correlations of life history traits.—One of the more hotly contested issues in evolutionary ecology is the adaptive significance of life history variation. Various theories have been proposed to relate both single life history traits and suites of correlated traits to particular adaptive strategies. Good reviews of these theories can be found in Wilbur et al. (1974) and Stearns (1976, 1977). Important messages of these articles are (1) that solid support for any of these general theories is lacking; (2) very different selective agents may produce adaptive phenotypes similar in appearance; and (3) lizards, among the best studied animals, fail to follow neatly the accepted schemes of life history evolution. We subscribe to these views and feel that data are not yet sufficient for *Sceloporus undulatus* to support any particular factor(s) as the selective agent(s) responsible for the observed geographic variation of life history traits. We therefore do not wish to champion any particular theory such as "*r*" and "*K*" selection, predation or bet-hedging; but rather we want to describe correlations that do occur in these life history traits and regional and latitudinal aspects of these correlations.

As pointed out previously, certain populations seem to have certain suites of traits including small body size, early maturity, short life span, small eggs, high clutch mass-body mass ratios, while others seem to have suites of the opposite character states (Tinkle 1969, Tinkle and Ballinger 1972). The eight populations with the most complete data were ranked for each trait and the ranks for all traits totalled. The eight populations were then compared on the basis of rank totals (Table 8). Certain geographic trends of these character suites were evident. First, of the four lowest ranking populations (large, late maturing, long lived, etc.), three are northern. Of the four highest ranking populations (small, early maturing, short lived, etc.), three are southern. All three grassland (desert grassland) populations rank high, while all three canyonland populations rank low. The eastern-woodland populations include low- and high-ranking populations. The Belvue, Kansas population is subject to high predation rates, relatively unlimited food, considerable variation in breeding success (caused chiefly by flooding), and temperature-influenced predation rates (see 2. Hatchling survival). According to several theoretical models, it should have evolved to a relatively high rank in the preceding traits, which it has.

A peculiar association that has not previously been reported was a negative one between clutch-size and body-size correlation and mean adult female size. Possibly the effect is ecological rather than genetic. Thus, the tightest correlation is in Kansas ($r = .86$), where food limitation seems relatively mild (this paper, Derickson 1976). If food competition is greater in other populations, many individuals in the latter populations may be producing fewer eggs than their physiological limit allows and the scatter around the clutch size-body size regressions would be greater. If this is true, correlation would become tighter with supplementary

feeding in the field or rich food supplies in the laboratory.

In conclusion, we take a somewhat paradoxical stand. On the one hand, we suggest that more basic studies of life history parameters on more populations are needed to round out our understanding of geographic variation. On the other hand, our knowledge of the predatory and competitive environments and other factors important in the ecology of most of these populations is meager. We know nothing of the genetic basis of any of these population differences. While we need more short-term studies on more populations, we need long-term, in-depth studies on single populations to weed out the adaptive significances and genetic bases of these life history strategies one by one.

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