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SEASONAL AND YEARLY FLUCTUATIONS IN CHIHUAHUAN DESERT LIZARD COMMUNITIES

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ABSTRACT: Two lizard communities, each consisting of seven residents plus several transient or immigrant species, were studied between 1970 and 1975 on a Chihuahuan desert watershed. Lizard species diversity was correlated with the previous 2 yr rainfall. H' varied between 1.28 and 1.91. The change in diversity in these lizard communities resulted from the influx of transient species and increase in numbers of resident species during a 2-yr wet period and the reverse during drought periods. The influx of transients and immigrants appeared to be related to the expansion of suitable habitat and the proximity to a source area for immigrants. The density of adult *Cnemidophorus tigris* nearly doubled in 1 yr which was attributed to above average overwinter survival of hatchlings. Seasonal activity periods of adults and hatchlings were longer during dry years than wet years. During wet years adults and juveniles of most species exhibited allochronic activity. Densities of most resident species varied directly with changes in productivity and relative abundance and activity of arthropods. *Sceloporus magister* numbers remained relatively constant over the 5 yr and this appeared to be related to availability of suitable habitat.

ALTHOUGH there have been numerous studies on the ecologies of lizards (e.g., Pianka, 1970) few studies have examined the dynamics of lizard communities over extended periods of time. Turner (1968) stated that it is particularly important that work on desert lizard populations be ex-

tended over a number of consecutive seasons. Long-term studies of entire lizard communities have rarely been undertaken because of time and manpower constraints. Due to these constraints, our understanding of factors affecting the dynamics of lizard communities is largely based on

fragmented autecological studies. In addition, recent interest in species diversity and factors acting as possible determinants of diversity have failed to consider the consequences of short-term changes in lizard community structure (Pianka, 1967, 1973).

In this paper we present data for two lizard communities inhabiting different ecosystems on the same watershed. Our studies encompass 5 yr of continuous data collection on all lizard species and provide the basis for understanding the relationships between changes in numbers of individuals and species composition and other components of the ecosystem.

METHODS AND MATERIALS

The study areas were established on a watershed draining the southeast slopes of Mt. Summerford of the Doña Ana range on the New Mexico State University Ranch, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. The watershed includes an alluvial fan (bajada) dissected by numerous ephemeral watercourses (arroyos) which drain into an ephemeral lake (playa). The soils on the bajada are shallow and sandy with the calcium carbonate deposition layer (caliche) occurring from a few centimetres to over a metre below the surface. The caliche layer is absent in arroyos which have complex soils varying from gravels to loam.

The vegetation is typical of large areas in the northern Chihuahuan desert. The well drained areas on the bajada have an essentially monotypic cover of creosotebush, *Larrea tridentata*, 23% cover, with all other species contributing \approx 1% cover. The arroyos are lined with a number of plant species including mesquite, *Prosopis glandulosa* (\approx 2% cover), tarbush, *Flourensia cernua* (1.5% cover), desert willow, *Chilopsis linearis* ($<$ 1% cover), apache plume, *Fallugia paradoxa* (0.8% cover) and two yuccas, *Yucca elata* (0.2% cover) and *Yucca baccata* (0.1% cover). The bajada slope varies from 5% to $<$ 1%.

At the lower end of the watershed, the

soils are deep sandy loams with grasses and forbs making up a significant part of the vegetative cover. Mesquite, is the dominant shrub on the periphery of the playa (14.7% cover) with morman tea, *Ephedra trifurca* (3.2% cover), snakeweed, *Gutierrezia sarothrae* (0.7% cover) and soaptree yucca, (0.25% cover) as associated species.

The playa bottom soils are fine clay-silts which alternately swell and crack depending on the degree of wetting and subsequent drying. The playa bottom has a cover of vine mesquite, *Panicum obtusum*, plus several species of forbs. At the soil transition between the playa and flood plain are dense stands of large mesquite, *P. glandulosa*.

Lizards were sampled by pitfall traps, noosing and hand capture. Pitfall traps were 40 cm deep, 30 cm in diameter and covered by an elevated wooden lid. Four 75 \times 150 m grids were established on the playa consisting of five lines with 10 traps per line at a 15-m trap interval. Half of the traps were on the playa bottom. On the bajada site a single 100-m² grid of 100 traps at 10-m intervals was established where the large drainage arroyo bisected the grid. Pitfall grids were examined daily during mid-summer and on alternate days during cooler periods. Periodic systematic searches (usually at 2-wk intervals) of both study sites were made to sample species by noosing and hand capture following established transect lines to insure sampling of all areas on the 30-ha playa site and 25-ha bajada site.

The following data were recorded for each lizard captured: weight (gm) using Pesola spring balances, snout-vent length (mm), location, date and time of capture. Each lizard was marked by toe clipping designed to provide unique identification of individuals. Population estimates were calculated by Lincoln Index using a 2-wk precensus and 2-wk census period. In species where densities and/or numbers recaptured were low, we used as a minimum

estimate the number of lizards captured during each time period. Data were corrected for area using $0.5 \times$ the mean recapture radius of a species added to the perimeter of pitfall grids. The area searched by transects was estimated as a belt 5 m wide multiplied by the distance walked on each transect.

An index of lizard species diversity (Poole, 1974), the Shannon-Weaver H' was calculated for each year using the June population estimates; $H' = - \sum_{i=1}^s p_i (\log p_i)$ where s = number of species and p_i = the proportion of the total number of individuals consisting of the i th species. June estimates were used because during that period all lizards had emerged from winter dormancy and hatching had not yet occurred.

The use of a combination of capture methods and several workers provided a large percentage of multiple recaptures for the more abundant species. For example, during the 5-yr study we handled between 180 and 260 adult *Cnemidophorus tigris* per year, of which between 19.3% and 34% were recaptured three or more times between 1 June and 31 July. More than 30% of the 50–80 adult *Phrynosoma cornutum* and *Holbrookia texana* handled each year were represented by two or more recaptures during the early summer sampling period. Density estimates for the other species were based primarily on the numbers of lizards handled. Occasional population estimates were made when there were sufficient recaptures to provide a reasonable estimate.

Our estimates of hatchling densities were, with few exceptions, based on numbers handled because of the low percentage of recaptures. Therefore, the density estimates of hatchlings and less abundant species are conservative and should be so interpreted.

Climatic data were recorded at standard weather stations on both the playa and bajada sites. Continuous recordings of air

temperature, relative humidity, rainfall, total incoming solar radiation and total wind were obtained and summarized for the entire study period (Whitford, 1971, 1972, 1973, and 1974).

Productivity of the dominant shrub species was estimated by dimension analysis in which growth increments of tagged stems were converted to biomass using equations developed by Ludwig et al., (1975). Productivity of other shrub species was estimated by harvest methods on 30 stratified, random plots on the playa bottom, 39 stratified, random points on the playa periphery and 25 stratified, random points on the bajada. These data were summarized and reported in Whitford (1971, 1972, 1973, and 1974).

A variety of methods were used to sample arthropods. Numbers of active colonies of ants were estimated at regular intervals using quadrat samples and point-quarter analysis (Whitford and Ettershank, 1975; Schumacher and Whitford, 1976). Surface active termites were estimated by belt transects and bait stations (Johnson and Whitford, 1975). Shrub, grass and forb arthropods were sampled at 2-wk intervals using a D-Vac® and Plexiglas® enclosure (Southwood, 1961). Relative abundance of grasshoppers, lepidopterans and other highly mobile arthropods were obtained by two persons walking flush transects (Whitford, 1972, 1973, 1974). The arthropods were identified to genus and species where possible or to family. Data were reported as density and biomass by Whitford (1973, 1974).

RESULTS

In the Chihuahuan desert the seasonal rainfall pattern as well as total amount of rainfall affects the primary productivity and hence the availability of arthropods as food for lizards. The 100-yr average rainfall \pm one standard deviation at the New Mexico State University Station is 211 ± 77 mm with most of that rainfall occurring during the summer from convective storms. Late autumn and winter rainfall

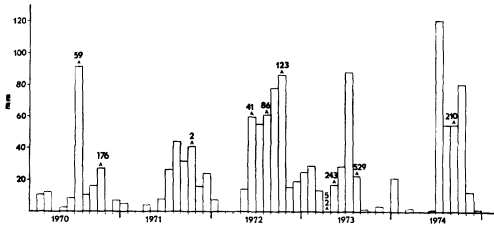


FIG. 1.—The pattern and amounts of rainfall recorded at the Jornada Validation Site 1970–1974, plus the standing crop biomass of grasses and forbs on the playa site. The biomass figures shown above the bars are in $\text{kg}\cdot\text{ha}^{-1}$.

in excess of 75 mm results in growth of spring annuals which are usually absent. Heavy precipitation in midsummer produces a flush of growth which results in relatively large biomass of grasses and forbs such as occurred in 1970 (Fig. 1). During the 1971 growing season, precipitation was characterized by a number of light rainfalls < 10 mm per event. This moisture quickly evaporated and resulted in little vegetative growth. From early summer 1972 through summer 1973, above average rainfall resulted in relatively high productivity in 1972 and even greater productivity of spring and summer annuals in 1973. The winter and early spring moisture in 1972 and 1973 resulted in the presence of growing forbs and grasses from late January through October (Fig. 1).

The pattern of plant productivity shown

in Fig. 1 is reflected in the estimates of arthropod biomass (Table 1). Although no quantitative estimates of Lepidoptera, Hymenoptera (other than ants and termites) and Orthoptera were made during 1971, these groups of arthropods which are available to nonarbooreal lizards were virtually absent during the summer of 1971 based on personal observations and field notes of co-workers.

Twelve species of lizards were recorded from the watershed during this study (Table 2). Resident species exhibited some habitat limitation but at times occurred as transients in other habitats. The nonresident species were immigrants from the more mesic habitats on the slopes of the mountain. Shifts in species composition during this study occurred during and immediately following periods of above-average rainfall when immigrant species became established members of the playa and bajada lizard communities (Fig. 2). The establishment of immigrant species accounted for a large part of the increase in the species diversity index of the playa lizard community (Table 3). Elimination of immigrant species in the calculation of H' reduced H' by 0.39 and 0.37 for playa lizards in 1973 and 1974 respectively, but decreased H' for 1973 bajada lizards by only 0.09.

Although there appeared to be a relation-

TABLE 1.—Arthropod biomass ($\text{g dry wt}\cdot\text{ha}^{-1}$) for time periods specified and for arthropod groups indicated (data from Whitford, 1971, 1972, 1973, 1974). Blank spaces indicate data not collected or samples not processed.

Area	Insect type	1971		1972		1973		1974	
		May	Aug	May	Aug	May	Aug	May	Aug
Playa	Shrub dwelling	17.2	54.6	3.1	175.7	8.9	57.7	---	---
	Lepidoptera and Hymenoptera	----	----	----	3.2	5.6	1.1	2.0	0.2
	Orthoptera	----	----	----	48.0	98.0	51.1	0.0	0.8
Bajada	Shrub dwelling	19.9	21.9	46.6	7.6	68.8	12.3	---	---
	Lepidoptera and Hymenoptera	----	----	----	0.1	0.3	0.3	0.9	0.5
	Orthoptera	----	----	----	10.0	25.0	100.0	0.0	0.0

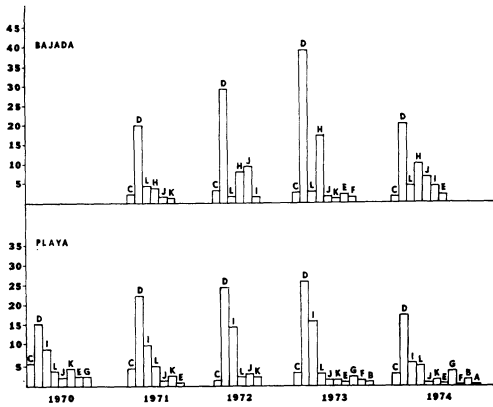


FIG. 2.—Pre-reproductive (early summer) densities of lizard species in a creosotebush community (bajada) and mesquite-yucca desert grassland community (playa). Species are as follows: A = *Cnemidophorus exsanguis*, B = *Cnemidophorus inornatus*, C = *Cnemidophorus tessellatus*, D = *Cnemidophorus tigris*, E = *Crotophytus wislizenii*, F = *Eumeces obsoletus*, G = *Holbrookia maculata*, H = *Holbrookia texana*, I = *Phrynosoma cornutum*, J = *Phrynosoma modestum*, K = *Sceloporus magister*, L = *Uta stansburiana*.

ship between changes in density of the more abundant species and rainfall, there were no significant correlations when June or July densities were regressed on the rainfall of the previous year or of the previous growing season. However, when the playa lizard species diversity index, H' (Table 3), was regressed on the average rainfall of the two preceding years, there

was a significant correlation ($r = 0.86$, $F = 19.2$, $p < .05$). The correlation between bajada species diversity and rainfall was not significant.

The density of adult *Cnemidophorus tigris* doubled in 1973 in comparison to the previous 2 yr (Fig. 3). This large increase may be due to larger clutch size in 1972 in response to supranormal rainfall as suggested by Pianka (1970) and rapid growth of 1972 juveniles resulting from favorable food resources. The bajada population returned to the 1971–1972 levels in 1974 but the playa density remained high (Fig. 3). Few hatchlings were seen in 1971 suggesting reduced clutch size (Pianka, 1970) and/or reduced hatching success and hatchling survival (Fig. 3). This resulted in little recruitment in 1972.

The bajada *Uta stansburiana* exhibited high reproductive success in 1972 and 1973 (Fig. 4). The low adult densities of *Uta* may reflect high turnover. The playa *U. stansburiana* exhibited a similar pattern of population change but lower densities of juveniles. On the playa in fall 1973 and early spring 1974, there was a high density, 20–25 ha⁻¹, of adult-sized *U. stansburiana* (Fig. 4). By midsummer most adults from the previous year had disappeared and the adult-size *Uta* were the young of the year.

The density of *Phrynosoma cornutum* on the playa remained relatively constant with

TABLE 2.—Habitat relationships of lizards on a Chihuahuan desert watershed. PR = permanent resident, T = transient resident from nearby habitat, I = immigrant from montane habitats.

Species	Playa grassland	Yucca-mesquite <i>Ephedra</i>	Open <i>Larrea</i>	Arroyo shrub association
<i>Cnemidophorus tigris</i>	T	PR	PR	T
<i>Cnemidophorus tessellatus</i>	T	PR	PR	T
<i>Cnemidophorus exsanguis</i>	I	I		
<i>Cnemidophorus inornatus</i>	I,T	I,T		
<i>Eumeces obsoletus</i>	I	I		I
<i>Holbrookia maculata</i>	T	T		
<i>Holbrookia texana</i>			T	PR
<i>Phrynosoma cornutum</i>	T	PR	T	T
<i>Phrynosoma modestum</i>		PR	PR	T
<i>Uta stansburiana</i>	T	PR	T	PR
<i>Sceloporus magister</i>	T	PR	T	T-PR
<i>Crotophytus wislizenii</i>		T-PR	T-PR	T-PR

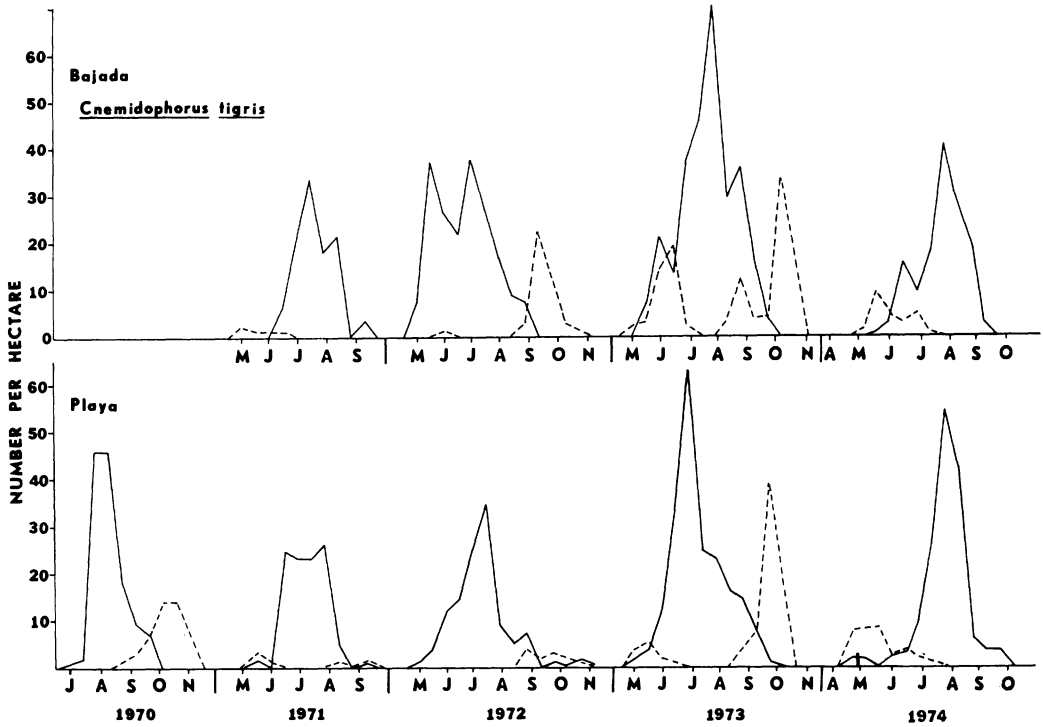


FIG. 3.—Comparison of yearly and seasonal fluctuations in density of *Cnemidophorus tigris* in two Chihuahuan desert ecosystems. Broken lines are data for subadults and juveniles.

what appeared as slight decreases in 1971 and 1974 (Fig. 5). These apparent decreases are probably sampling errors due to reduced activity during drought periods. The changes in density of *Holbrookia texana* were similar to those of *C. tigris* (Figs. 2 and 3). High reproductive success in *H. texana* in 1972 resulted in near doubling of density in 1973 but little change between 1973 and 1974 (Fig. 5).

TABLE 3.—Changes in the Shannon-Weaver diversity index (H') and number of lizard species (N) on the playa and bajada study areas from 1970 through 1974. H' was computed using June density estimates for each year.

Year	Playa		Bajada	
	N	H'	N	H'
1970	8	1.89	---	---
1971	7	1.54	6	1.34
1972	6	1.36	6	1.47
1973	10	1.64	8	1.28
1974	11	1.91	6	1.62

When the seasonal dynamics of individual species are considered, two obvious patterns emerge. First adults and juveniles of all species except *P. cornutum* exhibited allochronic seasonal activity. Numbers of active juveniles were greatest in the late summer and early fall: the hatchlings of the year. Juveniles also emerged before overwintering adults in the spring (Figs. 3–5). Second, all species in the community except *Uta* began and ended activity within the same 2-wk period. However, the duration of activity of the playa lizards was shorter than that of the bajada lizards (Figs. 3–5).

The earlier activity of the bajada lizards resulted in earlier hatching and hence a longer growth period prior to winter dormancy than playa lizards. Hatchlings appeared on the bajada up to 6 wk prior to the appearance of hatchlings on the playa. Bajada juveniles weighed $\approx 25\%$ more than playa juveniles of the same species in Sep-

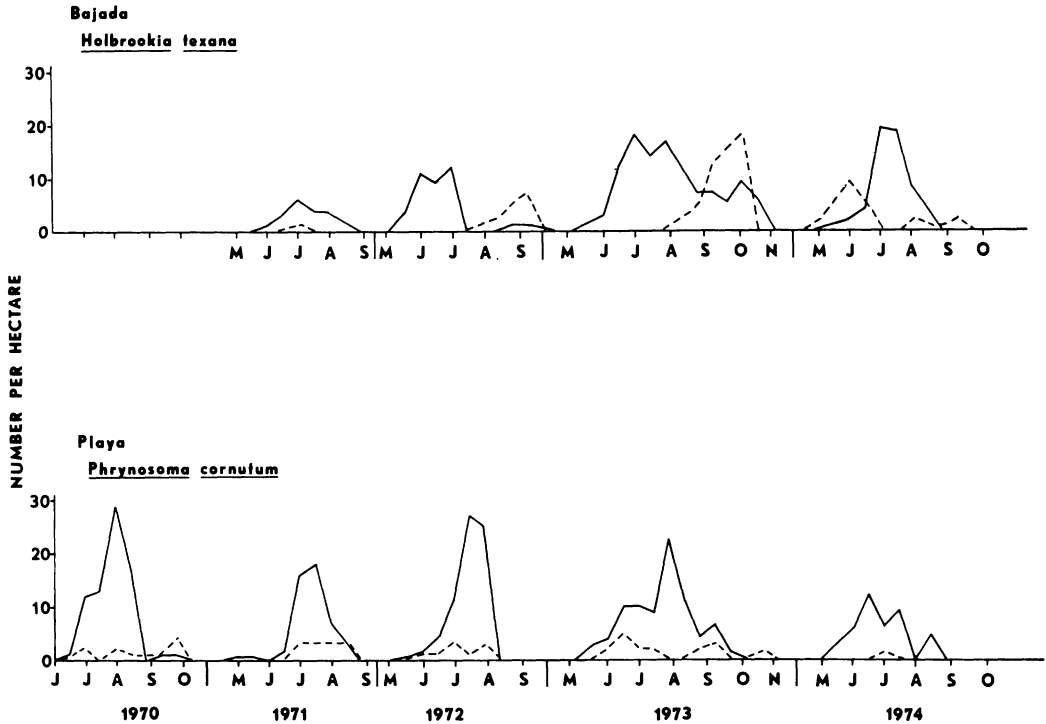


FIG. 4.—Yearly and seasonal fluctuations in density of *Holbrookia texana* and *Phrynosoma cornutum* in different Chihuahuan desert ecosystems. Broken lines are data for subadults and juveniles.

tember. The drought years, 1971 and 1974, apparently affected reproductive success since recruitment of juveniles was virtually absent during the late summer and early fall of those years (Figs. 3–5).

Seasonal activity and reproductive success, in most species, was closely related to food availability, which affected the physiological state of the animals. For example, in June and July 1971, *P. cornutum* had a mean weight loss of $1.02 \text{ g} \cdot \text{wk}^{-1}$ ($n = 12$). During that period, harvester ants and other species of ants were essentially inactive (Whitford and Ettershank, 1975) and thus *P. cornutum* was deprived of its primary food and water source. Other species exhibited some weight loss during this period, but not as consistent nor dramatic as that experienced by *P. cornutum*. Even during extreme drought conditions, some arthropods were available to lizards which are food general-

ists (Whitford and Ettershank, 1975; Johnson and Whitford, 1975; Table 1). *Cnemidophorus tigris* and *H. texana* responded to increased availability of arthropods in late summer and the following spring by increased recruitment of the young into the population producing peak prehatching densities in June and July, 1973 (Figs. 3–5). Playa populations of *U. stansburiana* responded to increased food by increased recruitment during 1973–1974, whereas bajada *U. stansburiana* appeared to exhibit little change in recruitment (Fig. 4).

The other permanent resident species exhibited little response to climatic conditions and food availability. Bajada *Phrynosoma modestum* exhibited fluctuations that were not related to availability of food and the playa production changed little during the entire study period. *Cnemidophorus tessellatus* exhibited a decline in numbers in

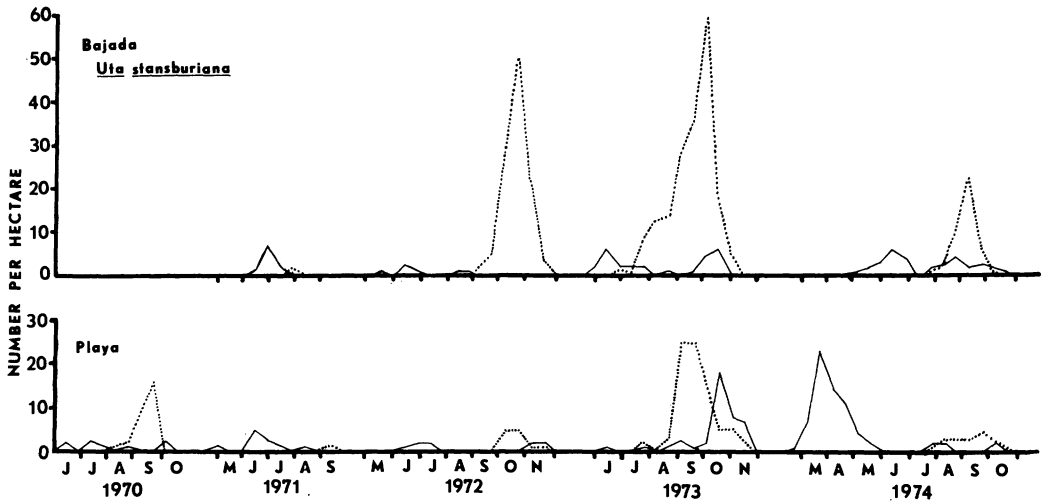


FIG. 5.—Comparison of yearly and seasonal fluctuations in density of *Uta stansburiana* in two Chihuahuan desert ecosystems. Broken lines are data for subadults and juveniles.

1972 reflecting the reduced food availability in 1971 (Fig. 2).

From 1972 to 1974 a special effort was made to mark and map the distribution of *Sceloporus magister*. Adult *S. magister* exhibited high fidelity to the large mesquite clumps (*Prosopis glandulosa*) along the edge of the playa. Mesquite clumps > 4 m in diameter, 2 m in height, which contained the large mound nests of packrats (*Neotoma* sp.) apparently provided sufficient habitat for individual *S. magister*. The only *S. magister* seen at more than 1 m from the "home clump" were hatchlings and some females during late June and early July. The number of adult *S. magister* was predictable from the number of large mesquite clumps which had packrat nests at the base. Four of the 15 adult *S. magister* marked in 1971 were found in their original mesquite clumps in 1974.

DISCUSSION

Climate, especially amounts and seasonal distribution of rainfall is unpredictable in the Chihuahuan desert (Houghton, 1972) resulting in marked differences in primary productivity and arthropod production and

activity from year to year. Fluctuations in rainfall amounts and seasonal distribution reported in this study were correlated with plant and arthropod productivity and reflected in the dynamics of the lizard communities. These effects are summarized in Fig. 6.

During the 18-m "wet" period starting in May 1972, several immigrant species became established on the desert sites. In addition, several resident species responded to the wetter conditions by increasing production. Immigrant establishment and enhanced recruitment of young of some resident species resulted in an increase in species diversity.

The importance of recent climatic history as a factor affecting diversity is supported by the correlation between the rainfall of the previous 2 yr and lizard species diversity. Pianka (1966, 1967) correlated diversity in desert lizard communities over a wide geographic area to growing season and spatial heterogeneity and to plant volume diversity. Within our watershed, spatial heterogeneity was increased somewhat during the wet period due to increased cover of annuals, and increased canopy of shrubs and perennial grasses.

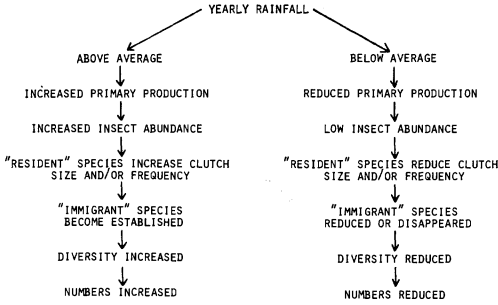


FIG. 6.—Scheme showing the relationship between rainfall and density and diversity of desert lizard communities. In areas remote from source areas, immigration would not be a factor.

This suggests that on a local scale, lizard diversity may increase with increased spatial heterogeneity but is probably more closely related to changes in habitat suitability. Since spatial heterogeneity is only one aspect of habitat, it is probably more instructive to examine population changes as a function of habitat change. During wet periods, more mesic habitat expanded from the sheltered slopes of Mt. Summerford to include both study areas.

Species such as *C. exsanguis* and *Eumeces obsoletus* which are usually confined to the more mesic environment of the mountain slopes became established on the study areas. *Cnemidophorus inornatus* apparently expanded its range from a grassy playa 2 km from the study area where this species appeared to be a permanent resident. Medica (1967) reported that, in a dry year, *C. inornatus* and *C. exsanguis* preferred wetter habitat and that during a wet year all of the *Cnemidophorus* he studied, except *C. exsanguis*, extended their range into habitats they had not occupied previous years.

The establishment of more mesic adapted species on our study areas and in Medica's (1967) study areas is a function of the proximity of those areas to a mesic source area. Such changes in diversity and species composition would not be expected to occur in areas more distant from a source area for immigrant species. These changes

are what one would predict, considering habitats as islands which change in character or size as suggested by the general theory of MacArthur and Wilson (1967), i.e., number of species is a function of island area.

There is a relationship between moisture, plant and arthropod productivity as reported in this study and a relationship between moisture and surface activity of ants and termites (Whitford and Ettershank, 1975; Schumacher and Whitford, 1976; Johnson and Whitford, 1975; W. Whitford and F. Creusere, *personal observations*). There are sufficient data in the literature on lizard diets that when food habits are considered with the data available from arthropod studies on the site, we contend that food availability was correlated with rainfall. Pianka (1970) showed that termites were the major food of *C. tigris* most of the season in desert flatland habitats and found a significant correlation between estimated lizard abundance and total precipitation during the previous 5 yr, an indicator of termite abundance. Medica (1967) also found an increase in whiptails during a wet year which he attributed to food and/or immigration. Based on that conclusion he suggested abundance was determined by food supply, which conclusion is supported by our data. Parker and Pianka (1975) showed southern *Uta stansburiana* eat, in order of importance, beetles, termites, grasshoppers, ants and insect larvae, and found a correlation between index of abundance and precipitation of the previous year. Pianka and Parker (1975) showed that ants make up 61.2% by volume of the diet of *P. cornutum*, and there is additional evidence (W. G. Whitford, *personal observations*) that *P. cornutum* in southern New Mexico feeds almost exclusively on harvester ants of the genus *Pogonomyrmex*. Although we found no published data on the food habits of *Holbrookia texana*, we observed this species feeding on flying insects and arthropods on the ground surface. Additionally,

Mayhew (1965, 1966a, b) has shown that in some lizards (*Uma*), reproduction is a function of rainfall and availability of insect food. Based on literature data and data presented in this study, we suggest that changes in lizard abundance and diversity are related to food availability as it affects suitability of habitat, reproduction and reproductive success.

The densities of lizards reported in this study are within the range of densities reported in the literature. Milstead (1965) reported densities of *C. tigris* between $45 \cdot \text{ha}^{-1}$ and $185 \cdot \text{ha}^{-1}$ in west Texas. Turner et al. (1969) reported densities of *C. tigris* between 8 and $20 \cdot \text{ha}^{-1}$ for southern Nevada. The large differences reported by Milstead (1965) were attributed to recovery from the effects of a severe drought, especially increase in vegetative cover. In our study, the population density of adult-sized *C. tigris* doubled during a 2-yr wet period. Turner et al. (1969) stated that year to year changes in density are to be expected but twofold fluctuations would be unusual. The twofold increase recorded in this study resulted from a low probability event, i.e., two successive years of above-average precipitation during the growing season which has occurred $2 \times$ in 100 yr (Houghton, 1972). A single wet year would probably have had much less effect on the density changes because we would expect lower early summer recruitment success as recorded in *C. tigris* in 1974.

The densities of *U. stansburiana* in these Chihuahuan desert ecosystems, are comparable to those reported by Tanner and Hopkin (1972) for three sites in Nye County, Nevada and slightly less than the lowest densities reported by Tinkle (1967) for the Kermit, Texas area. The Kermit, Texas area appears to provide nearly ideal habitat for *Uta* and supports low densities of only three other lizards. Differences in densities may be due to interspecific competition, productivity, predation or habitat suitability. The pattern of shifts in age structure and survivorship and density of

U. stansburiana is the pattern expected in a lizard which has been shown to have an annual population turnover (Tinkle, 1967).

Ballinger (1974) and Howard (1974) allude to stable population density in *P. cornutum* but provide no data to support this contention. Ballinger (1974) suggested that a high mortality rate of hatchlings would account for a stable population density in a species with low adult turnover. We encountered considerable difficulty in estimating densities of juvenile *P. cornutum* because we recorded few recaptures. Although our estimates of juvenile density in the late summer are undoubtedly conservative, the lack of recaptures suggests a high mortality of juveniles. Since juvenile horned lizards are easily captured, the probability of recapture of juveniles should be the same as adults but were, in fact, considerably less.

The greater overwintering survivorship in *U. stansburiana*, *H. texana* and *C. tigris* during the wet period, 1972–1973, we attribute to food availability. More abundant food allows greater fat deposition in juveniles prior to winter dormancy. Pre-winter dormancy fat accumulation can also account for allochronic activity between adult and juvenile lizards. After egg deposition adult lizards can feed and accumulate the fat stores necessary for winter dormancy. Accumulating such stores as rapidly as possible and entering dormancy before the onset of low temperatures reduces the probability of death by predation or accident. The data in Milstead (1957), Tinkle (1955), Parker (1972) and Medica (1967) suggest adults disappeared soon after the appearance of juveniles. Degenhardt (1966) recorded little or no disappearance of adults with appearance of juveniles. Data from this study shed light on these apparent inconsistencies. In years with high insect abundances, adults disappeared early in the summer but in years with low insect abundance, adults remained active well into the late summer. Such a pattern is consistent with the hypothesis

that disappearance of adult lizards of many species occurs as a result of physiological readiness for winter dormancy.

The seasonal differences in emergence time between bajada and playa lizards is directly attributable to climate. The playa acts as a cold air sink and the last frost (temperature $< 0^{\circ}\text{C}$) is from 3 to 4 wk later in spring and earlier in fall on the playa than on the bajada (Whitford, 1971, 1972, 1973). The earlier appearance of hatchlings on the bajada is also related to this difference in seasonality.

The marked weight losses in *P. cornutum* in 1971 are directly related to the lack of availability of the preferred prey, harvester ants. Whitford and Ettershank (1975) showed that few colonies of harvester ants were active during 1971. The only ants which were consistently active during the day were *Formica perpilosa* which nest at the base of, and forage in mesquite (*Prosopis glandulosa*), hence are not available to a nonarboreal lizard (Schumacher and Whitford, 1974). Milstead (1965) showed that, under drought conditions, termites made up a high percentage of the diet of *C. tigris*. Surface activities of termites are curtailed under drought conditions (Johnson and Whitford, 1975) which, in addition to the lack of alternate prey, probably accounts for the weight losses in *C. tigris* during early summer 1971.

The stable population size in *S. magister* is attributable to its territoriality. Tanner and Krogh (1973) and Parker and Pianka (1973) document the territoriality of this species and discuss its arboreal habit and foraging on ants. At the playa, mesquite clumps with associated packrat nests provide arboreal basking sites, protection from predators and abundant food in the form of ants *F. perpilosa*, *Myrmecocystus* sp., *Conomyrma* sp. and *Iridomyrmex* sp. which forage for exudates in mesquite throughout the growing season. Even during extreme dry periods, *F. perpilosa* and *Conomyrma* sp. forage in these clumps throughout the

day (Schumacher and Whitford, 1974; W. Whitford and F. Creusere, *personal observations*). Therefore, *S. magister* had a continuous supply of food even during drought.

As suggested previously, seasonal rainfall distribution and amounts appear to be the most important factors affecting Chihuahuan desert lizards. All species of lizards studied feed on arthropods, the abundance of which has been shown to be related to moisture. It is suggested that overwinter survival and egg production the following spring are related to lipid deposition, hence food supply, as discussed for *C. tigris* (Gaffney and Fitzpatrick, 1973), *Uma* (Mayhew, 1965, 1966a, b) and *Phrynosoma cornutum* (Ballinger, 1974). We suggest that seasonal activity of adult lizards is a function of food availability and that lizards enter dormancy after laying down sufficient fat stores for the winter dormancy period. It is further suggested that overwinter survival of juveniles is a function of food availability which determines fat stores for winter dormancy. While we realize that these are tentative conclusions based on indirect evidence from observational studies, they provide the rationale for manipulative studies which may further support these hypotheses.

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