Ecology 51: 703-720. (1970)

COMPARATIVE AUTECOLOGY OF THE LIZARD *CNEMIDOPHORUS TIGRIS* IN DIFFERENT PARTS OF ITS GEOGRAPHIC RANGE[1]

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Abstract. I studied various aspects of the life history of *Cnemidophorus tigris* over much of its geographic range, from southern Idaho through southern Arizona and into northern Sonora.

In the northern parts of its range, *Cnemidophorus* usually emerge from hibernation in May, and most adults aestivate during the midsummer months, but in the south the animals are active from April through late August. The seasonal period of activity is therefore considerably shorter in the north. Daily periods of activity are of similar duration from north to south, although the time of emergence tends to be later on northern areas. There is a significant positive correlation between estimated abundance and the total precipitation during the last 5 years, suggesting that the abundance of this species is determined by food supply. There is a latitudinal cline in the mean body temperature of active lizards, with northern populations being active at lower air and body temperatures. Whereas termites constitute the major food of southern lizards, beetles and grasshoppers are the primary food of northern lizards. Some seasonal dietary trends are described. The numbers and biomass of predatory lizards, birds, and snakes increase from north to south; correlated with this is a latitudinal increase in the percentage of lizards with broken regenerated tails. Hence there is probably greater predation on southern lizards. The length of fat bodies in *C. tigris* is not correlated with latitude but shows an inverse correlation with the long-term average annual precipitation. It is suggested that lizards from less productive areas must allow themselves a greater margin of safety due to the more probable occurrence of drought. Northern lizards breed only once during the short northern season but lay significantly larger clutches than southern lizards, which lay at least two clutches annually. Clutch size appears to be flexible in response to feeding conditions; on one study area with a low long-term mean precipitation, females laid larger clutches during the second year, after supranormal rainfall. There is a significant correlation between mean number of eggs per clutch and the deviation of the short term (last 5 years) mean precipitation from the long-term mean precipitation. A number of facts suggest that there was a decided population "crash" on one study area during the period of study. Competition is briefly discussed and it is suggested that if there is any latitudinal trend, it is most likely in the direction of greater competition among southern lizards.

In the conclusions, I suggest that the ecological challenges facing the northern populations are primarily physical, largely climatic ones, whereas biotic interactions (particularly predation) assume relatively greater importance to southern lizards.

Presumably, the common purpose underlying autecological studies is to accumulate data and information on a variety of species, allowing the eventual construction of a more general theoretical framework transcending the facts found for individual species. It is, therefore, desirable to examine the autecologies of a relatively complete taxonomic cross-section. Many workers have investigated the ecologies of iguanid lizards (Blair 1960; Crenshaw 1955; Fitch 1940, 1956; Gates 1963; Hirth 1963; Johnson 1965; Mayhew 1963, 1967; Norris 1949, 1953; Stebbins 1944a, 1944b; Tinkle 1967, 1969a; Tinkle, McGregor, and Sumner 1962). However, there are relatively few detailed studies of the ecologies of lizards belonging to other families. In particular, there are not many ecological investigations of teiid lizards (Fitch 1958; Hardy 1962; Hillman 1969; Hirth 1963; McCoy 1966; Medica 1967; Milstead 1957a, 1957b). This study, which was originally part of another investigation, is presented because it may help fill this gap, and because *Cnemidophorus tigris* nicely illustrates several ecological principles.

Cnemidophorus tigris extends from southern Idaho well into Mexico (Figure 1, adapted from Burt 1931; Stebbins 1954, 1966; and Zweifel 1962). Although 12 subspecies have been named (Burger 1950, Smith and Burger 1949, Zweifel 1958), 3 of which are island endemics in the Gulf of California, the species is still in need of further revision (Stebbins 1954, Zweifel 1962). Approximate ranges of the nine currently recognized mainland subspecies are shown in Figure 1. This study extends over much of the range of *Cnemidophorus tigris,* but deals with only three subspecies (*tigris, gracilis,* and *aethiops*). Milstead (1957a, 1957b, 1961, 1965) examined several aspects of the ecology of the subspecies *marmoratus* in western Texas. McCoy (1966) investigated *septentrionalis* in detail in Colorado. Other

[1] Received December 16, 1969; accepted April 16, 1970.

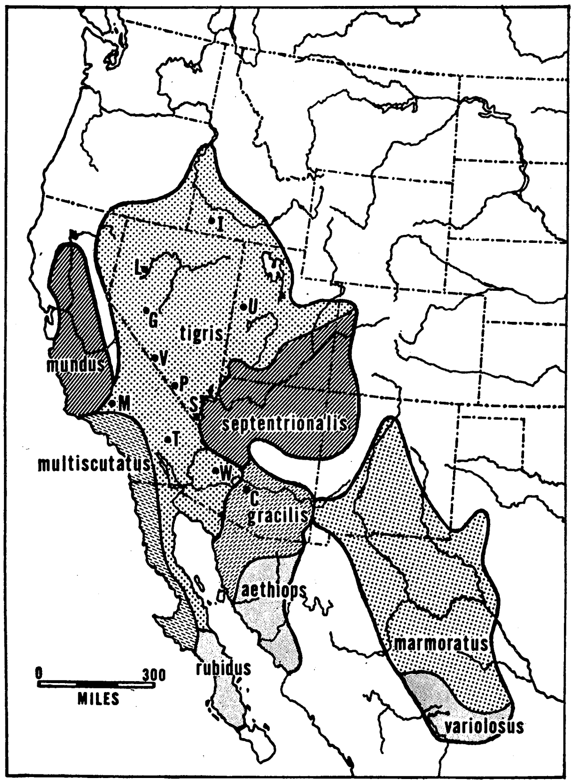

FIG. 1. Range map showing approximate geographic distribution of various mainland races of *Cnemidophorus tigris*. Lettered dots indicate the approximate positions of major study areas.

workers who studied various facies of the life history and distribution of *Cnemidophorus tigris* are: Allred, Beck, and Jorgensen 1963; Fautin 1946; Jorgensen and Tanner 1963; McCoy and Hoddenbach 1966; Pack 1923; Stuart 1932; Tanner and Jorgensen 1963; Tinkle 1959; Turner et al. 1969; Urban 1965; Willard 1966; and Zweifel 1962. The literature on the species up to 1930 was summarized by Burt (1931).

Burt (op. cit.) emphasized the wide variety of habitats inhabited by *tigris* throughout its extensive range, and noted that it occurs in sandy, gravelly, and rocky areas in desert flats, along bases of mountains and well up into mountain ranges. He emphasized that *tigris* is most abundant in deserts, and that if any habitat could be considered to be primary, it would be the extensive desert flats, where this species is usually one of the most common lizards. In the northern parts of its range (the Great Basin desert), *C. tigris* is practically restricted to the warm desert flats (which themselves are at high elevations), whereas further south it ranges up into higher country. Burt noted that *tigris* is commonest on areas with loose soils (in the southern parts of its range), but that it occupies areas with firmer hard-packed soils in reduced abundance. The species is found in digger pine-oak associations in California, in mesquite-yucca associations or on alkali flats in New Mexico, and in mesquite-saguaro associations in Arizona (Stebbins 1954). Zweifel (1962) found *C. tigris* in grassy situations in western New Mexico, and emphasized that it prefers open areas. It ranges from 81 m below sea level in Death Valley up to elevations of over 1,500 m on the high desert flats of the Great Basin. All in all, *C. tigris* is a very plastic and adaptable lizard, which thrives in a wide variety of habitats. Most of these habitats support a rather open vegetation and all of them occur in either desert or near-desert situations.

STUDY AREAS AND METHODS

The deserts of the western United States and northern Mexico form an enclosed, continuous series, uninterrupted by major physical barriers, over a latitudinal extent of nearly 1,600 km. Various workers have mapped the approximate boundaries of the Great Basin (Banta 1962), the Mojave (Shreve 1942), and the Sonoran deserts (Shreve 1951). Some authors also distinguish a separate region, the "Colorado desert," occupying approximately the zone of contact of the Mojave and Sonoran deserts; however, the Colorado desert has never been adequately defined and its biological distinctiveness is not universally accepted. Flatland desert habitats are common throughout the desert series, and are well suited for quantitative analysis because they usually occur in large homogeneous tracts. My study areas (most are shown in Fig. 1) are all located on desert flats, either in valleys or on gently sloping bajadas with contour intervals of no more than 9–15 m/km. All study sites cover from 15.5 to 52 km^2 of uninterrupted flatland desert. Area U in western Utah represents the location of the three areas reported on by Fautin (1946), who gives *Cnemidophorus tigris* abundances and relatively complete supporting information on plants and other animals in this area.

The most common perennial plants on the seven southernmost study areas are *Larrea divaricata* and *Franseria dumosa,* while *Atriplex confertifolia* and *Sarcobatus vermiculatus* predominate in the Great Basin. *Artemisia tridentata* is abundant at higher elevations and on the slopes of mountains, but is seldom found on the warm saline desert flats. There is an increase in the number of life forms of perennial plants from north to south along the desert series. The Great Basin desert usually has only one or two plant life forms, all very densely packed small semishrubs; the Mojave desert nearly always supports two or more life forms, adding larger woody perennials such as *Larrea divaricata* to the small semishrubs. There may be as many as 10–15 different plant life forms in the arboreal Sonoran desert (Shreve 1936, 1942). The structural complexity of the vegetation is thus much greater in the southern deserts than in the more northern deserts. On 10 desert sites, my estimates of the percentage cover vary from 6.0 to 20.0% (Pianka 1967). More information on some of the study areas and their floras and faunas can be found in my unpublished thesis (Pianka 1965).

The major latitudinal trend in the thermal climate is the progressive lowering of both average monthly temperatures and average hourly temperatures as one proceeds northwards. The length of the frost-free period ("growing season") generally becomes shorter towards the north. Figure 2 illustrates the annual change in the average daily range of temperature. From June to about October, the daily range in temperature (mean maximum minus mean minimum daily temperature) is greater in the north than in the south. This variable changes more or less gradually and continuously with latitude, although the amplitude of diurnal fluctuations in temperature tends to be depressed locally near larger bodies of water, such as Hawthorne Lake, Lake Mojave, and Pyramid Lake.

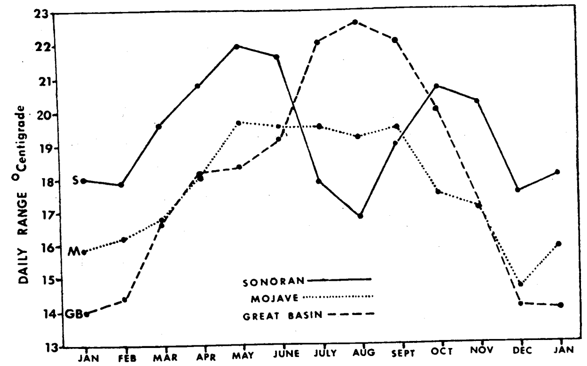

FIG. 2. Annual march of average daily range in temperature, for selected stations representative of each desert.

Annual patterns of rainfall vary widely along the desert series. A biennial pattern of rainfall characterizes the Sonoran desert, as the 6-month-long dry summer season does the Mojave desert. In the Great Basin, precipitation is usually spread fairly evenly over the year, although there are local variations due to the basin and range topography. Torrential rains fall in the Sonoran desert in July and August, frequently causing flash floods. The striking feature of these rains is that they are extremely localized, falling on a limited extent of desert, while adjacent regions receive little or no rain. Water supply becomes more predictable closer to major water channel beds (which are usually dry) due to channeling of run-off water. Winter precipitation in all three deserts is characteristically more gentle and allows better utilization by desert plants, except when it occurs as snow.

A noteworthy feature of desert ecology is the strong correlation between total annual precipitation and net above-ground primary production; this correlation has been demonstrated for several different regions including North American and African deserts (Blaisdell 1958; Pearson 1965; Walter 1939, 1964). There is probably a direct causal basis to this widespread relationship, since water is almost certainly the "master" limiting factor in most deserts (see also Rosenzweig 1968). The degree to which precipitation and production are correlated depends upon both the temperature and the amount of water lost from the system by run-off and evaporation. Neither run-off nor evaporation varies appreciably during the growing season along the desert series of western North America (Visher 1954); it is thus possible to use precipitation data to estimate the amount and variability of primary production. A variety of climatological parameters calculated from U.S. Weather Bureau data have already been published (Pianka 1967), with the distance between the study area and the weather station used as the source of the data. Hastings (1964) and Hastings and Humphrey (1969) provide data from weather stations near my study areas in Sonora, Mexico.

The northernmost Great Basin was surveyed in June and July of 1962 and area I visited twice during this time. March through August of 1963 were spent in the Sonoran and Mojave deserts, collecting on areas M, T, W, and C. Each of these study areas was sampled every 2 or 3 weeks, in an attempt to assess seasonal changes. Since monthly samples proved to be adequate, during the next season, from March through August, 1964, areas were usually visited at approximately monthly intervals. During the 1964 period, three of the 1963 areas (M, T, and C) were revisited at the beginning and end of the season, and area C was also sampled once during the middle of the season. Five new sites were established in 1964 and each visited three times (one was sampled four times) during the season (May–June, June–July, and July–August). These five new areas were areas L, G, V, P, and S. During the summer of 1969 limited observations were made on *Cnemidophorus tigris aethiops* in the Mexican state of Sonora on areas A and B. Exact coordinates, section numbers and altitude of most of the areas studied can be found in Pianka (1965) or obtained from the author. Approximate positions of the major study areas and of Fautin's (1946) three areas are plotted in Figure 1.

In this investigation, I have relied upon periodic sampling of unmarked populations, as this approach maximized the amount of information gathered per unit of time and effort. My statistics are therefore populational, and provide little or no data on such aspects as territories, home ranges, survivorship, growth or mating behavior; however a certain amount of the information obtained can be applied to individuals. Other workers have marked and recaptured *Cnemidophorus tigris* individuals and examined abundance, longevity, and home range (Degenhart 1966, Jorgensen and Tanner 1963, McCoy 1966, Turner et al. 1969). McCoy's study is particularly complete. Their data complement the findings presented here.

Lizards were observed and collected while my assistants and I made transects through the habitat, recording distances covered with a leg pedometer. Walks were normally started before and continued until near the end of *Cnemidophorus* activity. Parameters recorded for every lizard encountered include: date, time, approximate size (small, medium, or large), position in the environment when first observed, and subsequent movements (including whether or not the lizard took fright and ran, or continued to walk or sit undisturbed). Using the first lizard seen as "time zero," the total number of lizards observed was divided by the total miles walked to estimate abundance. The effective width of the transects was estimated at roughly 15–25 feet (4.6–7.6 m); a strip 20 feet (6.1 m) wide by 1 mile (1.6 km) long is very close to 1 hectare. Through the remainder of this paper I have converted the units from the number per man-mile to the approximate number of lizards per hectare. Sources of bias and error are further discussed in the results section.

When possible, lizards were shot and collected, and these specimens supplied data on sex, weight, exact size (snout-vent length), body temperature, tail length and whether or not the tail had been broken and regenerated. Dissection of the preserved material yielded information on the length of the fat bodies, gonad condition (the length of the testes in males, the average size and total number of eggs in females), and stomach contents. Estimates were made of the numbers and volumes of food items in 21 different categories for each lizard stomach. Volumes of intact stomachs were estimated to one-tenth of a cubic centimeter by volume displacement, using a small graduated cylinder. The approximate volume of individual prey items was then estimated visually, to the nearest one-hundredth of a cubic centimeter, by the proportion of the total stomach volume taken up by a given prey type. Individual prey items in each lizard stomach were counted. Food categories used in this study are listed in Tables 2 and 3. Food species diversities were calculated with Shannon's (1949) information theory measure, $-\Sigma p_i \log_e p_i$ where p_i is the proportion of prey in the i^{th} category.

Body temperatures of active lizards were recorded with a Schultheis cloacal thermometer as soon as possible after capture. If the delay between shooting and capture was unduly long or the lizard was badly damaged, its body temperature was not recorded. During the morning hours (when the lizards are most active), the rate of change of temperature is similar in all three deserts, and closely approximates a straight line (Pianka 1965, 1967). Air temperature was therefore measured at intervals during several hours of collecting, and, assuming linearity, the air temperature for each lizard was estimated from the time of observation. No attempt was made to measure microclimatic features of the environment such as substrate temperatures, and I can make no estimate of the thermal diversity available to the lizards. Incident radiation and substrate temperatures may frequently be a more important determinant of body temperature than absolute air temperature (Bogert 1949, Pearson 1954, Willard 1966). During the course of this study, some 2,962 *Cnemidophorus tigris* were observed, and 2,020 collected and dissected.

Both the nonparametric Spearman rank correlation coefficient (symbol r_s) and the Pearson product moment correlation coefficient (symbol r) are used. Calculation and significance of the former statistic follows Snedecor (1956) and Siegel (1956). Parametric statistics and tests (t-test, F-test, and correlation coefficients) are calculated from formulas and tested with tables in Fisher (1958) and Fisher and Yates (1963). Standard symbols are used for the mean ($\bar{x}$), standard deviation (s), sample size (N), and standard error of the mean (SE) in the text and tables.

RESULTS AND DISCUSSION

Abundance and seasonal activity patterns

The first *Cnemidophorus* seen on any given day was used to begin the transect and count. Although this procedure somewhat overestimates abundance, the error is always in the same direction and should be slight, as several days and many miles of walking were used for each estimate. My abundance estimates represent minimal figures because all of the lizards are probably not active at any given time. It is possible that individuals might emerge only on every other day and that the population could be twice as large as estimated. There are distinct seasonal differences in the activity patterns of males and females (see also section on reproduction); hence observed abundance is always somewhat lower than actual abundance. However, relative differences in abundance from site to site should be reflected even by these crude estimates, which were always taken during the morning "warming-up" period when the greatest number of lizards are active. Figure 3 shows the observed abundances on the study areas for each visit and gives the average abundance through the season (except for the northern areas I, G, L, and V, see below).

Fautin (1946) and Tanner and Jorgensen (1963) present evidence that in the northern parts

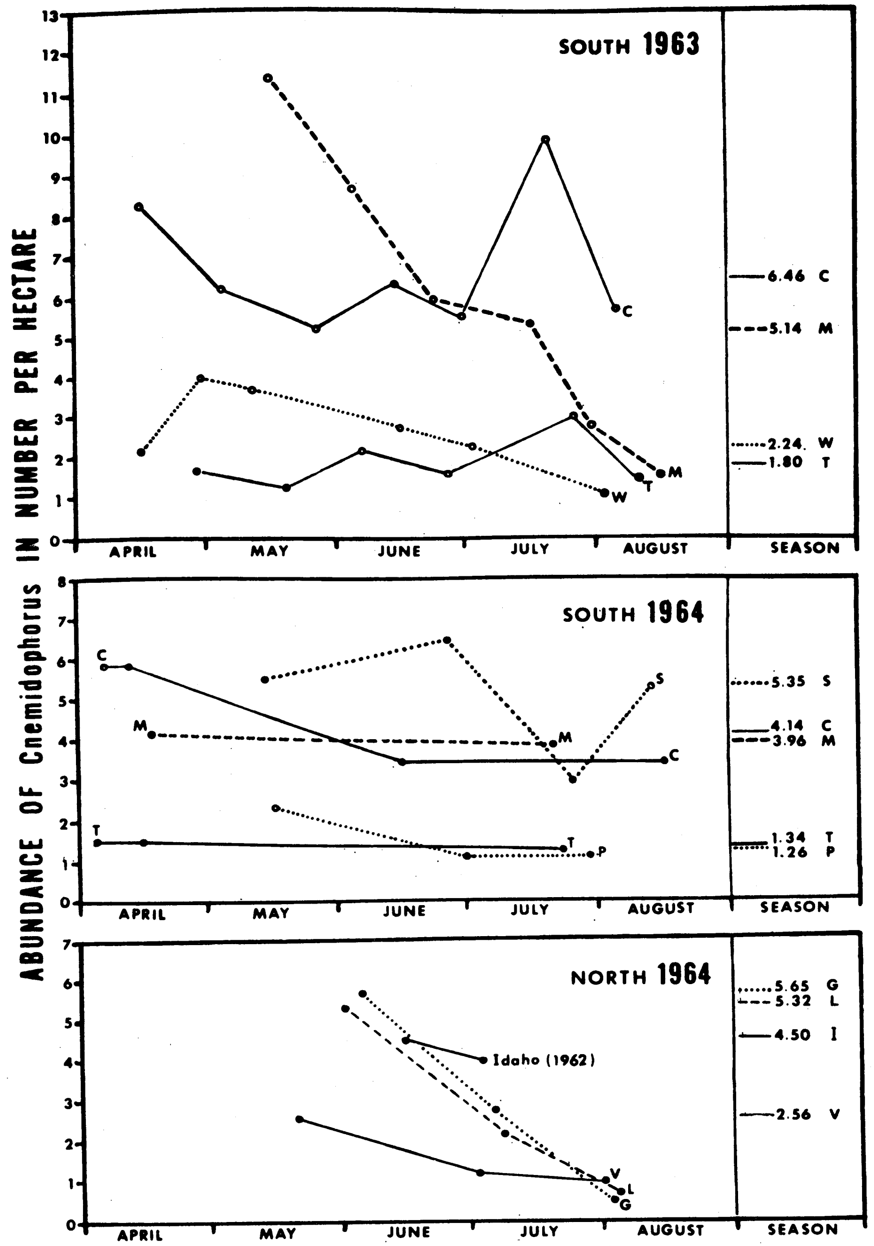

FIG. 3. Estimated *Cnemidophorus* abundances on the study areas during the seasons (see text).

of its range, *Cnemidophorus tigris* aestivate during the late summer months. Fitch (1958) showed the same for *Cnemidophorus sexlineatus* in Kansas. Populations of *tigris* in the Mojave and Sonoran desert are active all summer, while more northern populations are most active during May and June and aestivate during July and August (Figure 3). (The southern M-area is a special case of a population "crash," to be considered later.) A few juveniles remain active in the north into mid-August, but most of the adults disappear. By means of capturing and recapturing marked individuals, Tanner and Jorgensen (1963) demonstrated higher natural mortality in nonaestivating than in aestivating individuals. Freedom from above-ground predation is a probable explanation for this observation, but does not explain the difference between northern and southern populations. The occurrence of summer rains might explain the continued activity of Sonoran desert populations, but there is usually less summer rain in the Mojave desert (with summer-long *Cnemidophorus* activity) than there is in the Great Basin desert (with summer aestivation). The wide range in daily temperature in the Great Basin during July, August, and September (Figure 2) might be forcing summer inactivity, but the exact causal sequence remains unclear. As a result of summer aestivation the effective "length of the season" for northern lizards is even shorter than that set by the length of the frost-free period. It is somewhat surprising that northern populations restrict themselves in this way, apparently reducing their energy budget. By contrast, the iguanid lizards *Uta stansburiana, Crotaphytus wislizenii,* and *Phrynosoma platyrhinos* all show continued activity from May through August in the Great Basin (Pianka unpublished data).

Because of these seasonal changes in activity, I used the abundances estimated in May or June (the breeding season, when activity is greatest) as the best estimates of the actual abundance on areas I, L, G, and V. Even though my estimates of abundance are crude, since almost nothing is known about the control of abundance in lizard populations, it is interesting to attempt to explain the observed differences between study sites. One hypothesis might be that abundance is regulated by food supply; because of the strong correlations between precipitation and production, the actual insect food available to lizards should be crudely reflected in precipitation parameters. Several potentially interesting measures of precipitation are: (1) the long-term average annual value, (2) the long-term average value for the growing season, (3) long-term average winter precipitation, and (4) various short-term values such as the total precipitation during the 12 months prior to the census. There is no correlation between the latter short-term value and *Cnemidophorus* abundance, but there are significant correlations with the long-term average annual precipitation ($r_s = .604$, $P < .05$) and with the total precipitation during the last 5 years ($r_s = .561$, $P < .05$). This is reasonable since *Cnemidophorus tigris* is a relatively long-lived lizard (Turner et al. (1969) report a mean life expectancy of about 3–4 years), and suggests that its abundance might be controlled by the amount of available food. Abundance is not significantly correlated with either the long-term average warm-season precipitation or the long-term mean winter precipitation.

Daily activity pattern, air temperature, and body temperature

Cnemidophorus tigris displays a bimodal diel pattern of activity, with many more individuals active during the morning warming-up period (between about 0700 and 1200) than during the afternoon cooling-off period. Actual times of emergence and duration of activity depend upon the season and local climatic conditions. In the early spring, when environmental temperatures are generally low, individuals emerge late in the morning (about 1100–1200) and display a single daily period of activity, whereas in the summer months they emerge early and retreat underground during the hottest part of the day. Similar seasonal shifts in daily activity patterns have been noted in other lizard species by Mayhew (1964) and Pianka (1969). There is no convenient graphic way of illustrating daily activity patterns, because they vary with local climatic conditions and during the season. However, there are invariably many fewer individuals abroad during the afternoon than during the morning, and almost all of my counts were made in the morning. The time of emergence is later in the north than in the south. The average air temperature at the time of capture of 276 northern lizards (from the I, L, G, and V areas) was 24.8°C ± .17, while that from 1,507 southern lizards (all other sites) was 27.5°C ± .14. The mean body temperature for northern lizards was also significantly lower (38.9°C ± .11; $N = 293$) than that for southern ones (39.7°C ± .04; $N = 1555$). This latitudinal shift in body temperature (see also Table 1) suggests that the lizards accommodate to the cooler environmental temperatures in the north by being active at lower body temperatures, in addition to being active later in the day, when ambient environmental tem-

TABLE 1. Statistics on time of activity, air temperature, and body temperature

Area	Time of collection[a]				Air temperature (°C)				Body temperature (°C)			
	$\bar{x}$[b]	s[c]	N[d]	SE[e]	$\bar{x}$	s	N	SE	$\bar{x}$	s	N	SE
I	10.4	2.28	60	0.29	23.9	3.61	58	0.47	38.4	2.43	77	0.28
L	10.1	1.67	85	0.18	24.7	2.40	81	0.27	38.7	1.80	80	0.20
G	10.2	2.18	63	0.27	24.2	2.51	58	0.33	39.2	1.32	60	0.17
V	9.9	1.31	80	0.15	25.9	2.43	79	0.27	39.3	1.82	76	0.21
P	9.4	1.72	91	0.18	26.9	4.01	86	0.43	39.4	1.65	85	0.18
S	9.1	1.59	190	0.12	28.8	2.44	184	0.18	39.0	1.81	181	0.13
M63	10.3	1.47	417	0.07	25.5	3.14	411	0.16	39.7	1.55	411	0.08
M64	10.4	1.46	81	0.16	25.0	4.70	81	0.52	39.5	1.27	80	0.14
T63	9.3	1.38	148	0.11	27.5	2.98	147	0.25	39.9	1.68	146	0.14
T64	9.3	0.75	38	0.12	27.8	5.50	38	0.89	38.6	1.45	36	0.24
W63	9.5	2.30	133	0.20	27.7	3.07	127	0.27	39.5	1.82	140	0.15
C63	9.9	1.98	358	0.10	30.3	4.27	321	0.24	40.4	2.57	364	0.13
C64	9.8	1.61	108	0.16	27.3	5.01	108	0.48	39.3	1.80	108	0.17
North	10.1	1.85	288	0.11	24.8	2.82	276	0.17	38.9	1.93	293	0.11
South	9.8	1.72	1,568	0.18	27.5	3.78	1,507	0.14	39.7	1.70	1,555	0.04

[a] in hundredths of an hour
[b] $\bar{x}$=mean
[c] s=standard deviation
[d] N=sample size
[e] SE=standard error of mean

peratures are most similar to those used by southern populations. Variances in time of collection, air temperature, and body temperature show no consistent latitudinal trends, indicating that the duration of the diurnal period of activity is similar in north and south (Table 1).

There is a loose insignificant correlation between mean air temperature and mean body temperature ($r_s = .389$, $P < .20$). The large amount of scatter is graphic illustration that these lizards regulate their body temperatures and they depend largely upon solar and substrate radiation, rather than upon the air, for their heat source (Bogert 1949, Willard 1966).

Foraging behavior and diet

All teiids which have been studied (*Ameiva, Cnemidophorus,* and *Dracaena*) forage similarly, by actively moving through the environment, constantly grubbing, digging, and frequently extending their tongues (Hirth 1963, Fitch 1958, Milstead 1957a, Rand 1964). *Cnemidophorus tigris* is a very active lizard, which forages by moving incessantly, progressing along in a somewhat jerky fashion from shrub to shrub, stopping now and then to dig through debris or to climb a short distance up into the base of a shrub for some particularly large food item such as lepidopteran larvae. They poke their snouts into every nook and cranny, and frequently protrude their tongues, appearing to depend largely upon olfactory cues for much of their feeding. Stebbins (1948), in his study of nasal anatomy of lizards, concluded that *Cnemidophorus tigris* has a keen sense of smell. Occasionally, when a lizard sees a more active prey item such as a grasshopper, it may stalk and make a short swift attack. The method of foraging does not vary noticeably from north to south, except that the lizards are searching underneath different shrub species in the various parts of their range. Most foraging is done in the litter accumulated underneath various shrubs, but some prey is captured in open areas between shrubs, too.

There is a pronounced latitudinal shift in the composition of the diet. Southern lizards eat large numbers of termites (Isoptera), while northern lizards rely on other food types and do not take many termites (Tables 2 and 3). It is possible, though not definitely established, that there simply are very few termites in the Great Basin flatland desert habitats. Fautin (1946) did not record termites from quantitative insect samples or from the stomachs of the lizards he examined in western Utah.

Distinct seasonal changes in diet occurred on all study areas (Figure 4). Some generalizations about these seasonal patterns are possible: insect larvae constitute an important food item in the spring for both northern and southern populations, but rapidly disappear as summer progresses. Termites are the major food item of southern *C. tigris* over most of the season, usually increasing in importance from April through August. Beetles form an important, often fairly constant, portion of the diet in both the north and south, frequently representing about 20% of the food by volume. The volumetric importance of grasshoppers remains low all year long in the southern diet, but reaches a peak during the summer months in

TABLE 2. Summary of the stomach contents of 313 *Cnemidophorus* from the four northern study areas (I, L, G, and V)

Prey category	Number	Volume	% total number	% total volume	Frequency
Spiders	53	7.2	1.9%	2.5%	.14
Scorpions	29	15.8	1.0%	5.4%	.09
Solpugids	6	3.0	.2%	1.0%	.02
Ants	58	1.2	2.0%	.4%	.04
Other Hymenoptera	4	.3	.1%	.1%	.01
Grasshoppers	308	90.4	10.7%	31.0%	.58
Roaches	3	.5	.1%	.2%	.01
Mantids	7	3.3	.2%	1.1%	.02
Ant lion adults	1	.2	.03%	.6%	.003
Adult beetles	481	52.2	16.8%	17.9%	.61
Termites	1,314[a]	11.6	45.8%	4.0%	.09
Homoptera–Hemiptera	2	.7	.1%	2.4%	.01
Diptera	12	1.2	.4%	0.4%	.03
Adult Lepidoptera	4	.8	.1%	.3%	.01
Insect eggs	96	.9	3.3%	.3%	.015
Pupae	4	.5	.1%	.2%	.01
All insect larvae	328	63.1	11.4%	21.6%	.45
Unidentified insects	137	13.0	4.8%	4.5%	.31
Lizards	11	5.4	0.4%	1.9%	.01
Vegetative material	7	.7	.2%	.2%	.02
Unidentifiable partially digested material	6	19.6	.2%	6.7%	.02
Totals	2,871	291.6			

[a] All termites are from V-area lizards

TABLE 3. Summary of the stomach contents of 1,608 *Cnemidophorus* from the six southernmost study areas (C, W, T, M, S, and P)

Prey category	Number	Volume	% total number	% total volume	Frequency
Spiders	222	22.8	.31%	1.61%	.106
Scorpions	12	5.3	.01%	.38%	.006
Solpugids	62	30.9	.09%	2.19%	.033
Ants	294	5.3	.41%	.37%	.069
Other Hymenoptera	37	5.3	.05%	.37%	.021
Grasshoppers	402	84.6	.56%	5.98%	.170
Roaches	354	75.2	.49%	5.32%	.149
Mantids	39	12.9	.05%	.91%	.024
Ant lion adults	29	4.0	.04%	.28%	.015
Adult beetles	2,569	219.3	3.58%	15.51%	.687
Termites	63,253	463.8	88.27%	32.79%	.787
Homoptera–Hemiptera	98	8.7	.13%	.62%	.034
Diptera	31	4.9	.04%	.35%	.016
Adult Lepidoptera	1,061	58.8	1.48%	4.16%	.092
Insect eggs	1,088	2.7	1.52%	.19%	.021
Pupae	14	2.0	.02%	.14%	.006
All insect larvae	1,453	223.4	2.03%	15.80%	.380
Unidentified	577	28.1	.81%	1.99%	.184
Lizards	23	51.3	.03%	3.63%	.013
Vegetative mateial	11	0.8	.02%	.06%	.004
Unidentified partially digested material	27	104.3	.04%	7.37%	.008
Totals	71,656	1,414.4			

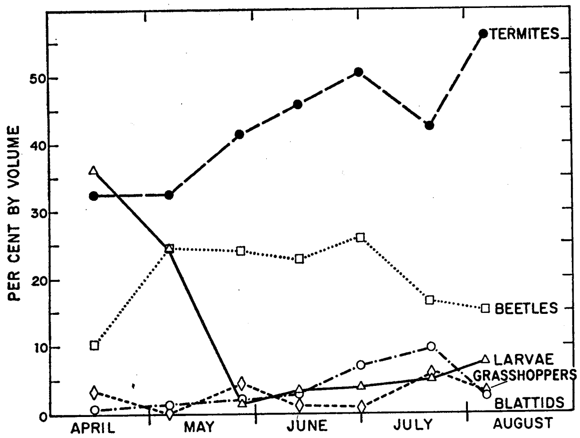

Fig. 4. Major food items of area C lizards during the 1963 season, showing the percentage of total stomach volume occupied by various prey types. Figure is based on stomach contents of 377 lizards.

Table 4. Numbers and volume food species diversities of *Cnemidophorus tigris* through the seasons indicated

Site	Year	Numbers food species diversities			Volume food species diversities		
		Males	Females	Total	Males	Females	Total
I	1962	1.289	1.496	1.428	1.304	1.489	1.459
L	1964	1.643	1.708	1.695	1.940	1.941	1.963
G	1964	1.460	1.478	1.488	1.719	1.783	1.787
V	1964	0.997	0.897	0.957	1.832	1.716	1.800
P	1964	0.668	0.642	0.662	2.083	1.908	2.047
S	1964	0.359	0.355	0.360	1.701	1.461	1.657
M	1963	0.894	0.950	0.918	2.126	2.255	2.203
M	1964	1.221	0.890	1.179	1.869	1.933	1.922
T	1963	0.361	0.360	0.363	1.890	1.815	1.892
T	1964	0.880	0.574	0.786	1.941	1.928	2.037
W	1963	0.478	0.397	0.439	1.962	1.843	1.938
C	1963	0.316	0.367	0.337	1.721	1.818	1.814
C	1964	0.513	0.841	0.635	1.726	1.766	1.785

northern populations. During July and August, the diet of nonaestivating northern lizards consists of approximately 50% grasshoppers by volume. It is interesting that the diets of other lizard species in the Mojave and Sonoran deserts such as *Uta stansburiana* and *Callisaurus draconoides* show a decided summer increase in the importance of grasshoppers (Pianka unpublished data). This suggests a midsummer peak of grasshopper abundance in both the northern and southern deserts, but in the south *Cnemidophorus* are not substantially exploiting this resource.

Food species diversities for the different populations, calculated using Shannon's (1949) measure of information, are listed in Table 4. There is little difference between sexes, but food species diversities (by numbers) reflect the latitudinal change in diet. The very high dietary diversity of the 1963 area M population is discussed later. Figure 5 shows the significant inverse correlation between food species diversity (by volume) and the short-term mean precipitation for the 5 years preceding study. These results indicate that where primary productivity is low, the lizards eat a wider variety of foods than they do where productivity is high. MacArthur and Pianka (1966), using a theoretical argument, predicted that where food is abundant, optimal diet should be more restricted than where it is less abundant; Figure 5 supports their prediction.

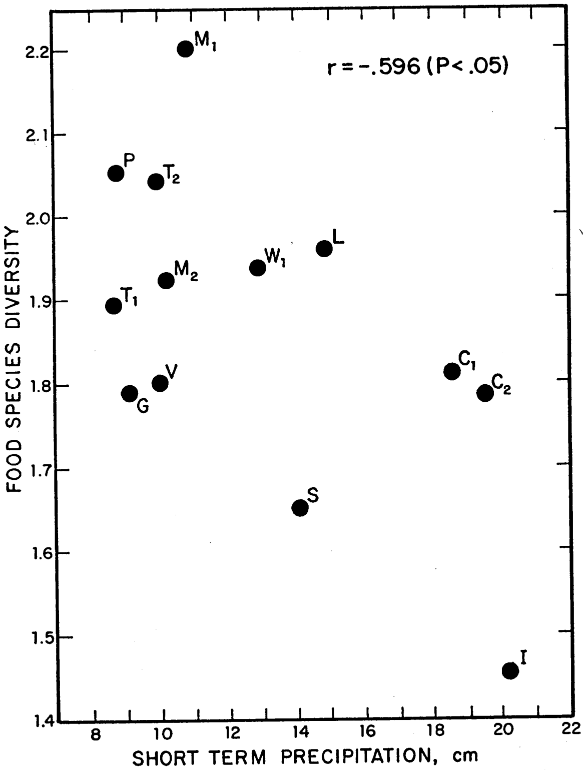

Fig. 5. Food species diversity (by volume) is plotted against the mean precipitation for the 5 years prior to study.

Predation, escape behavior, and broken tails

Because most lizards are primary and secondary carnivores, accurate data on the intensity of predation on them is difficult to obtain. A number of carnivores which prey upon *Cnemidophorus* have been identified by finding remains of the lizards in the predator's stomachs, and/or by direct observation of predation. Burt (1931) lists as known "enemies" of *C. tigris* the roadrunner (*Geococcyx californianus*), the leopard lizard (*Crotaphytus wislizenii*), the collared lizard (*Crotaphytus collaris*), and the following snakes: *Masticophis flagellum, M. taeniatus, Crotalus cerastes,* and *C. tigris*. Klauber (1956) adds the following rattlesnakes to the list: *Crotalus scutulatus, C. mitchelli, C. ruber,* and *C. viridis*. Stebbins (1954)

TABLE 5. Data on lizard-eating snakes from 1963 and 1964. *Chionactis occipitalis,* which does not eat lizards, is omitted from the totals

Snake species	C[a]	W	T	M	S	P	V	G	L	I
Crotalus cerastes	7	6	10	3	1	3				
Crotalus scutulatus	3	1		2	2					
Crotalus atrox	1	1								
Crotalus viridis								?	1	?
Masticophis flagellum	1	1	2	4	1	1	4	1	1	
Masticophis taeniatus										1
Pituophis catenifer	3	?		1	1			?	1	?
Salvadora hexalepis	?	1				1	1			
Rhinocheilus lecontei	1			2	1					?
Arizona elegans	4	?	2				1			
Lampropeltis getulus californiae							1			
Phyllorhynchus	3									
Chionactis occipitalis			2	1			2		1	
Total number	23	10	14	12	6	5	7	1	3	1
Kilometers covered	328	153	251	224	103	134	122	80	92	56
Number per km	.070	.065	.069	.054	.058	.037	.057	.012	.033	.017
Probable no. of species	9	7	3	5	5	3	4	2	4	3?

[a]Study sites are listed in order of increasing latitude.

TABLE 6. Lizard-eating bird counts (number seen)

Bird species	C[a]	W	T	M	S	P	V	G	L	I
Toxostoma (all species)	19	4	26	19	3	2				
Speotyto cunicularia	3	?	1	1						
Lanius ludovicianus	4	7	2		2	1				
Geococcyx californianus	2	2	1	1						
Buteo (all species)	3	2								
Falco mexicanus									4	
Falco sparverius	1			1						
Corvus species			+	+					+	
Total number of birds	32	15	30+	22+	5	3	0	0	4+	0
Total km walked	328	153	251	224	103	134	122	80	92	56
Number per km	.098	.098	.120	.098	.071	.022	.00	.00	.044	.00
Total number of species	7	4	4+	4+	2	2	0	0	1+	0

[a]Study sites are listed in order of increasing latitude.

says that the snakes *Salvadora hexalepis, Pituophis catenifer,* and *Rhinocheilus lecontei* have all been recorded to prey on *Cnemidophorus* species, and indicates that *Arizona elegans, Phyllorhynchus decurtatus, Hypsiglena torquata,* and *Lampropeltis getulus californiae* also eat various lizards. Thus, it may be safely assumed that practically all of the larger snakes occurring in areas with *C. tigris* will, on occasion, prey upon it. Another lizard which is known to eat *Cnemidophorus* is the Gila monster, *Heloderma suspectum* (Bogert and Martin Del Campo 1956). In addition, various raptorial birds and shrikes must be considered potentially important predators.

Two independent estimates of the intensity of predation indicate higher rates of predation on southern populations (Tables 5, 6, and 7). During the present study every predatory bird and snake observed was identified, if possible, and recorded, and those noted during collecting walks allow crude estimation of the relative number of predators per unit area on each of the study sites. Tables 5 and 6 summarize these data, showing a roughly three-fold increase in the number of predatory snake species and a strong increase in the number of species of avian predators from north to south. There is also a pronounced north-to-south increase in the number of individual predators (Tables 5 and 6) and in total predator biomass per unit area (Pianka unpublished). Hence, predation pressures on *Cnemidophorus tigris* may be potentially greater in the southern deserts. Data on broken and regenerated tails for males, females, and both sexes combined are presented in Table 7, showing that females often have slightly higher frequencies of broken tails than males; but there is no significant statistical difference between the sexes. There is no correlation between abundance and the percentage of broken tails; therefore differences between populations in such percentages probably reflect real differences in the amount of predation and are not merely due to increased intraspecific fighting and aggression. The latitudinal trend in the percentage of broken and regenerated tails (Table 7) is significant at the 5% level ($r = -.516$). It is notable that area M was discrepant during both years it was sampled, showing exceptionally low broken tail frequencies. Possible reasons for this are presented later.

There were significant behavioral differences between the populations studied in their reactions to the human predator (my research assistants and myself). This fact can be shown in several different, independent ways; the most convincing is the percentage of lizards observed which were actually collected. Figure 6 shows the significant inverse correlation between estimated abundance (number per hectare) and percentage collected ($r_s = -.642$, $P < .05$).

Lizards from wetter, more productive areas (where *Cnemidophorus* are more abundant) are generally harder to approach and capture and much more wary than those from drier less productive areas (where the lizards are not as abundant). It may be argued that on productive areas where food is dense the lizards can afford to spend more time and energy on predator avoidance than they can in areas with barely enough food to maintain themselves. Indeed, this is the easiest way to explain the observation that lizards from populations with high percentages of broken tails, and thus presumably with intense predation, are sometimes fairly easily collected (e.g., area W). Alternatively, the relatively high density of lizards on more productive areas may in itself support

TABLE 7. Percentages of broken regenerated tails in *Cnemidophorus tigris*

Area	Year	Latitude	Males		Females		Combined	
			N	%	*N*	%	*N*	%
I.............	1962	42° 12′	45	37%	39	32%	84	35%
L.............	1964	40° 12′	36	28%	49	18%	85	22%
G.............	1964	38° 48′	25	36%	34	41%	59	39%
V.............	1964	37° 05′	43	40%	37	43%	80	41%
P.............	1964	36° 18′	54	46%	37	43%	91	45%
S.............	1964	35° 18′	124	47%	69	46%	193	47%
M.............	1963	35° 06′	233	25%	183	29%	416	27%
M.............	1964	35° 06′	40	23%	41	32%	81	27%
T.............	1963	34° 08′	81	53%	69	62%	150	57%
T.............	1964	34° 08′	24	54%	13	46%	37	51%
W.............	1963	33° 41′	79	46%	66	53%	146	49%
W.............	1964	33° 41′	3	67%	1	100%	4	75%
C.............	1963	32° 57′	226	39%	149	42%	375	40%
C.............	1964	32° 57′	65	46%	45	49%	110	47%
B.............	1969	29° 38′	47	36%	24	58%	71	44%
A.............	1969	28° 20′	18	72%	8	50%	26	65%

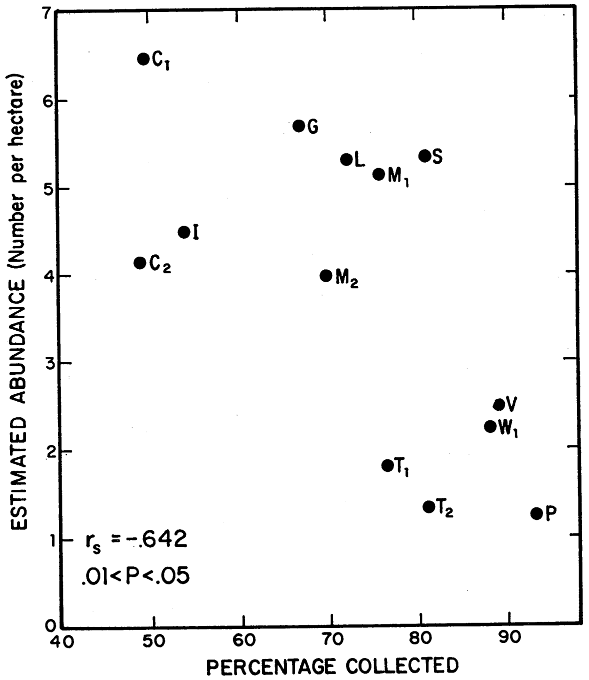

FIG. 6. Estimated abundance of *Cnemidophorus* plotted against the percentage of those sighted which were collected. This graph indicates, as do several other independent kinds of analyses, that on areas where the lizards are more common, they are more difficult to approach and collect.

more predators, whereas the lower density on less productive areas may usually preclude the maintenance of many predators.

Fat bodies

Cnemidophorus tigris have large fat storage organs protruding into the coelom from the ventral pelvic region, which vary in size during the season and from area to area. In the analysis presented below, the lengths of both fat bodies were measured to the nearest millimeter, and the sum used. This procedure somewhat underestimates the volume of the largest fat bodies, but still allows demonstration of some significant differences between populations. Presumably a more refined volumetric analysis would merely amplify these patterns.

While the usual trend in northern populations is for the fat bodies to increase more or less continously in size during the season, just the reverse is true of southern lizards (Pianka unpublished data). This difference is probably causally related to the occurrence of second clutches in southern populations (see next section); Hahn and Tinkle (1965) related fat body cycling to follicle development in *Uta stansburiana.*

There is no correlation between mean fat body size and latitude. Surprisingly, however, the largest fat bodies occur in lizards from sites with the lowest long-term annual precipitation, rather than from the areas of greater precipitation as might have been predicted (Figure 7). A similar, though not as good, inverse correlation exists with short-term measures of precipitation. These data suggest that lizards from the less productive areas allow themselves a greater margin of safety, presumably due to the more probable occurrence of drought. The greater range in mean fat body sizes on study areas with low long-term mean precipitation values also suggests this interpretation (Figure 7). Such a mechanism would require a genetic basis in order to persist. There are, however, other possible explanations for a shift in the energy budget with changes in the average amount of production. For instance, in-

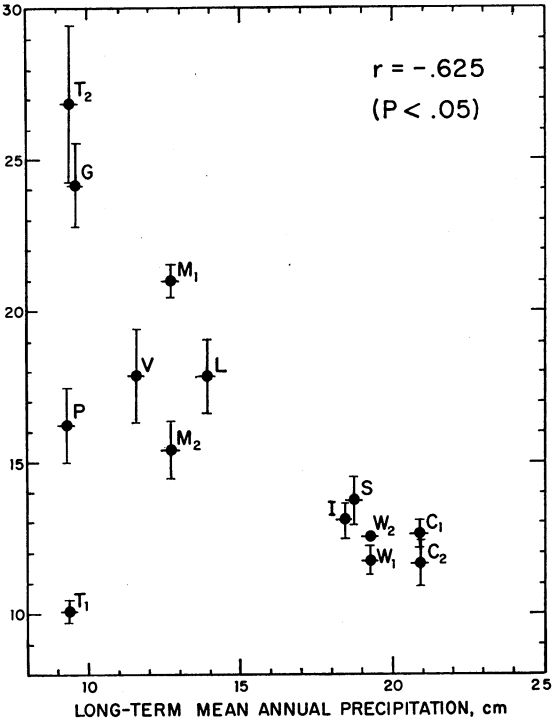

FIG. 7. A plot of the mean length of the fat bodies against the long-term average annual precipitation, suggesting that lizards occurring on less productive areas allow themselves a greater "margin of safety." Means plotted as dots; one standard error above and below the mean is shown by the vertical lines.

creased predation in more productive areas might require greater energy expenditure on predator avoidance, and thus reduced fat reserves.

Reproduction

Observed sex ratios of *tigris* are usually slightly biased towards males in the spring, near equality in June, and slightly biased towards females during the late summer months. This reflects a sexual difference in activity patterns, rather than an annual differential mortality, because many of the lizards survive 3 or 4 years in nature. Apparently some gravid females retire underground until their eggs are ready for deposition, and do not emerge again until late summer.

Mating activities were observed frequently during the study, during May and early June. There is only one fairly short annual cycle of breeding on northern areas, but at least two periods of breeding occur each year in the southernmost populations. Milstead's (1957a) observation of mating in late June and late July indicates that the Texas subspecies *marmoratus* has two breeding periods (or at least one more extended period). McCoy and Hoddenbach (1966) present evidence that, whereas a Colorado population laid only one clutch, a Texas population laid two clutches per year. This is not surprising, since the length of the frost-free period is nearly twice as long in western Texas (about 200 days) as it is in the Great Basin (about 120 days). The longest growing seasons, however, occur around the head of the Gulf of California (Visher 1954), a region with very low precipitation (and hence low primary production), which may not usually allow breeding during the late summer.

Tinkle (1969b) asserts that the age of first reproduction in *Cnemidophorus tigris* is only 1 year in Texas, but 2 years in Nevada. The smallest females I have seen in reproductive condition measure 71 mm snout to vent. It may be that, because of the short seasonal period of activity of northern lizards, it requires two seasons to reach this size in the north but only one season in the south.

In my samples, oviducal eggs occur from mid-April through late July on southern areas. On northern areas the frequency of oviducal eggs is usually greatest during late May and early June. In the Great Basin and Mojave deserts, testes volumes are large in April, May, and June, decreasing sharply during July. These data indicate late spring–early summer mating in northern populations. In the Sonoran desert, however, testes volumes increase slightly in late July, no doubt a reflection of the second clutch in southern populations.

Because of the inactivity of females carrying large oviducal eggs, it is difficult to obtain samples large enough to make reliable estimates of the average clutch size. However, earlier in the season, before the eggs have been ovulated, these same females are actively feeding and larger samples can be collected. When the average number of follicles per female is plotted against egg size categories, each of which includes all larger egg classes, Figure 8 is obtained. Sample size, therefore, decreases rapidly as egg size is increased. This kind of analysis was performed for females from each study area; but for ease of comparison, in Figure 8 the four northernmost and the six southernmost areas are grouped. A noteworthy feature of these plots is the sharpness of the breaking point between the number of smaller and larger eggs at about 3 mm and the nearly straight line beyond that point. Only a few follicles enlarge to 4 mm, and the number of eggs which will ultimately be ovulated can be estimated by the number of ovarian eggs over 4 mm (ovulation takes place when the eggs are between 10 and 12 mm). Apparently there is little follicular atresia once the

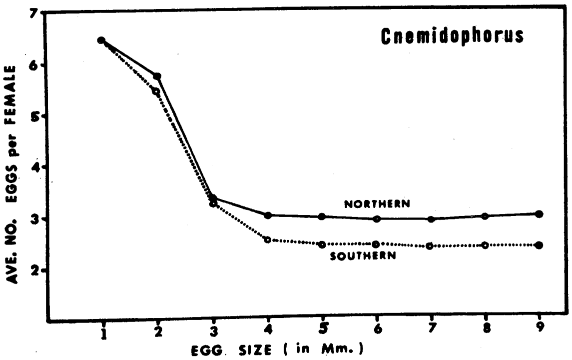

FIG. 8. The mean number of eggs per female is plotted for all eggs above the size given on the abscissa (diameter). Sample size thus decreases rapidly from left to right. Northern lizards have a significantly larger clutch than southern ones. Complete statistics on clutch size are given in Table 8.

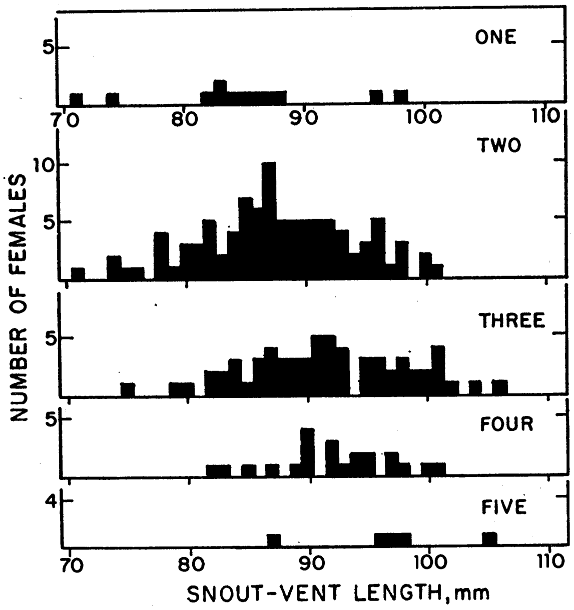

FIG. 9. Frequency distributions of snout-vent lengths for females laying one, two, three, four and five eggs, respectively, showing that larger lizards tend to lay more eggs per clutch. However, 80% of the females lay only 2 or 3 eggs at a time.

eggs have reached 4 mm, when they begin to become yolked. Therefore the best estimate of clutch size is the average number of ovarian (and oviducal) eggs per female which are over 4 mm.

Clutch size varies from one to five eggs and is only loosely correlated with the body size of the female (Figure 9). The average egg number per female ranged only from 2.29 to 3.43 on 10 study areas. Table 8 gives statistics for all eggs 4 mm and over. (It is noteworthy that there was no reproduction on area M during 1964: more is made of this fact later.) Although the combined northern lizards have a significantly larger mean clutch size than the combined southern lizards (t-test, $P < .05$), area-by-area correlation is very loose and inconsistent (see Table 8), suggesting that there may not be a causal connection. Probably more meaningful is the correlation ($r_s = .65$, $P < .05$) between the average number of eggs per female and the deviation of the short-term (last 5 years) mean precipitation from the long-term mean values (Figure 10). On area T mean clutch size in 1963 (a dry year) was 2.3, but in 1964 (a very wet year) the average clutch was 3.4 eggs per female, an average increase of over an egg per female. The response of these females to supranormal rainfall suggests that clutch size can be varied according to feeding conditions. Zweifel and Lowe (1966), Mayhew (1967), and Hoddenbach and Turner (1968) have related reproductive status to recent rainfall in *Xantusia, Uma,* and *Uta,* respectively.

Figure 10 demonstrates that lizards on areas with less than the long-term average annual rainfall during the past 5 years generally had smaller than average clutches, whereas those from the areas which had received more than the long-term average rainfall had larger clutches. By coincidence, the four northern sites had closer to normal or supranormal precipitation than did the six southern sites during the 5 years preceding this study, and consequently it is not known whether larger clutches are really characteristic of northern populations. However, these data support Lack's (1954) generalization that clutch size is regulated by food availability. Although there is no parental care after the eggs are deposited, females must expend considerable amounts of energy producing the large yolky eggs.

The area M population crash

In the preceding pages, I frequently note that circumstances were peculiar on area M during the period of study. There was a very sharp decline in estimated population size during 1963 and a fairly constant, much lower, population in 1964 (see Figure 3). It would be difficult to distinguish this "crash" from seasonal inactivity, were it not for the second year's observations. The population level during 1964 remained steady at about 4 lizards per hectare, a much lower figure than during the previous year, when up to 11.4 lizards per hectare were counted. It may be significant that the latter figure constitutes the highest abundance recorded during this study, a possible indication that the population had exceeded the carrying capacity of the area. A number of separate lines of evidence support this conclusion. As pointed out in the discussion on reproduction,

TABLE 8. Clutch size statistics for *Cnemidophorus tigris* (all eggs 4 mm and over)

Site	Number with eggs N_e	Total number N_t	Per cent with eggs	Mean clutch size $\bar{x}$	Standard deviation s	Standard error of mean SE	Coefficient of variation $s/\bar{x}$
I	29	39	74%	2.93	0.923	0.171	0.315
L	6	49	12%	3.00	1.095	0.447	0.365
G	6	36	17%	3.17	1.169	0.477	0.369
V	12	37	32%	3.00	0.853	0.246	0.284
P	9	37	24%	2.56	0.527	0.176	0.206
S	22	69	32%	2.32	0.568	0.121	0.245
M-63	46	184	25%	2.37	1.554	0.229	0.656
M-64	0	41	0%	—	—	—	—
T-63	7	69	10%	2.29	0.756	0.286	0.331
T-64	7	13	54%	3.43	1.134	0.429	0.333
W-63	18	67	27%	2.44	0.856	0.202	0.350
C-63	25	149	17%	2.68	1.249	0.450	0.266
C-64	14	45	31%	2.64	0.745	0.199	0.282
North	53	161	33%	2.98	0.930	0.128	0.312
South	149	675	22%	2.51	1.149	0.094	0.458
Total	202	836	24%	2.63	1.113	0.078	0.423

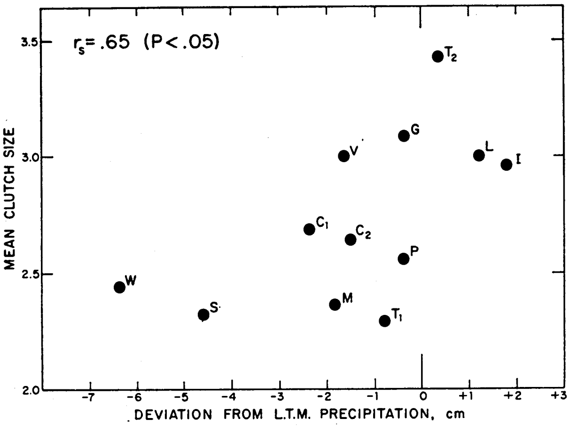

FIG. 10. Plot showing correlation between mean clutch size and short-term (last 5 years) deviation from the long-term precipitation. Table 8 gives complete statistics on clutch size.

there was no egg-laying in a sample of 41 females from this population in 1964. Furthermore, the variance in snout-vent length (*F*-test) and the mean size of fat bodies (*t*-test) decreased significantly from 1963 to 1964. The diversity of stomach contents by volume increased from 1.49 to 2.15 during 1963 and stayed high during 1964, suggesting poor feeding conditions (see Figure 5 and MacArthur and Pianka 1966).

All these changes could be indicative of a genuine "crash" in this *Cnemidophorus* population. Examination of the precipitation record for Mojave, California (6–8 km away) shows a prolonged 4-year drought from 1959–1962, preceded by 2 years (1957–1958) of markedly above-average precipitation. The following tentative sequence is proposed: during the 2 good years 1957 and 1958, recruitment was high and a large population was built up. For some unknown reason the subsequent drought did not decimate the population until 1963. There was supranormal precipitation during 1963, but this came after the *Cnemidophorus* population had crashed, and much of it was lost as runoff. The year 1964 was one of the driest on record, with only a third the long-term average precipitation, presumably making survival, let alone reproduction, difficult. However, it should be noted that two other lizard species, *Uta stansburiana* and *Callisaurus draconoides,* did not show population "crashes" during the period of this study. Perhaps shorter life spans preclude such delayed "time lag" effects as appear to be operating in the *Cnemidophorus* population.

Competition

As I have outlined elsewhere (Pianka 1967), the number of species of syntopic lizards increases from 4 to 10 along a latitudinal transect from Idaho to southern Arizona, with a sharp increase at the border of the Great Basin and Mojave deserts. It is convenient to use this boundary as a breaking point to distinguish "northern" from "southern" lizard assemblages. Thus defined, only 5 species of lizards coexist in the northern flatland desert, while from 6 to 10 species may occur together in various southern flatland desert communities.

Exact positions of every lizard observed during this study were noted; those running when first sighted are not used in the analysis to follow. Table 9 summarizes the percentage utilization of 10 microhabitat elements by all the species of liz-

TABLE 9. Percentages of utilization of various microhabitat elements in northern and southern deserts, based on the locations of lizards when first sighted

	Larrea		Other shrubs		Open		Trees		Rocks		
Species	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	*N*
North											
Cnemidophorus	9.6	3.6	21.4	8.2	55.9		0.9	0.5			220
Uta	3.5	1.2	11.1	2.9	41.3	1.7	6.4	2.3	29.1	0.6	172
Phrynosoma			1.3	1.3	96.1	1.3					77
Crotaphytus	1.9	1.0	14.3	9.5	65.7	1.0	1.9	1.0	3.8		105
Callisaurus	3.0		1.0	1.0	73.3				21.7		101
South											
Cnemidophorus	29.8	6.0	5.2	1.3	46.5		8.5	2.8			1,511
Uta	42.7	5.3	5.0	2.5	21.5	0.2	17.2	4.5	0.7		617
Phrynosoma	3.6	1.8	1.8		83.9	7.1	1.8				56
Crotaphytus	29.7	5.4	5.4	2.7	45.8		10.8				37
Callisaurus	7.4	1.7	1.1	0.6	86.3		1.7	1.1			175
Sceloporus	1.2	1.2	2.4	3.7	7.3		50.0	34.2			82
Urosaurus	15.7		3.0		6.1		48.4	27.6			33
Dipsosaurus	28.4	3.9	8.8	2.9	50.0	1.0	3.9	1.0			102
Uma	4.9		2.4	7.3	80.5	2.4	2.4				41
Coleonyx		4.6				90.9		4.6			44
Xantusia								100.0			27

TABLE 10. Shannon information theory measures of food species diversities (by volume) and microhabitat diversities for the lizard species coexisting with *Cnemidophorus* in various parts of its geographic range

	Food niche breadth		Place niche breadth	
	North	South	North	South
Cnemidophorus tigris	2.01	2.15	1.27	1.40
Uta stansburiana	2.05	2.24	1.60	1.58
Crotaphytus wislizenii	1.99	0.62	1.19	1.37
Phrynosoma platyrhinos	1.26	1.48	0.21	0.67
Callisaurus draconoides	2.00	2.30	0.76	0.59
Sceloporus magister		1.05		1.37
Urosaurus graciosus		2.12		1.27
Dipsosaurus dorsalis		1.29		1.22
Uma scoparia		1.79		0.79
Coleonyx variegatus		1.98		0.37
Xantusia vigilis		1.69		0.00
Heloderma suspectum		low		?

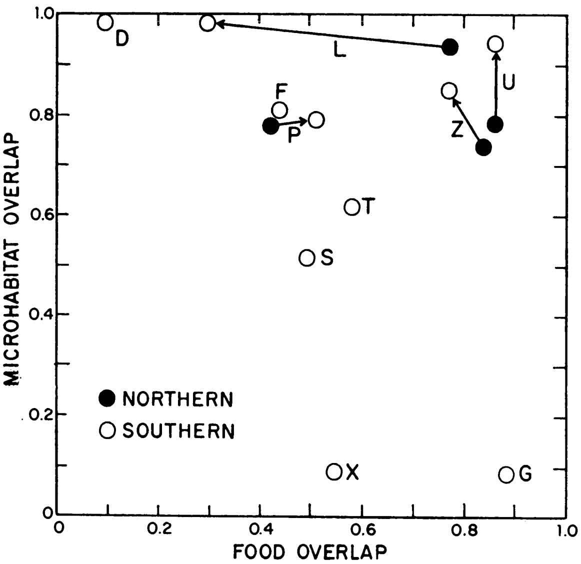

FIG. 11. Graphic portrayal of dietary and microhabitat overlap of *Cnemidophorus* with other potentially competing lizard species, showing changes from north to south. The overlap index used is Horn's (1966) R_0 (see text). D = *Diposaurus dorsalis,* L = *Crotaphytus wislizenii,* U = *Uta stansburiana,* Z = *Callisaurus draconoides,* F = *Uma scoparia,* P = *Phrynosoma platyrhinos,* S = *Sceloporus magister,* T = *Urosaurus graciosus,* X = *Xantusia vigilis,* and G = *Coleonyx variegata.*

ards involved. Table 10 lists the Shannon information theory measure, *H,* for food species diversity (by volume; Pianka unpublished data) and for microhabitat diversity (from Table 9) for the species concerned. These parameters measure the food and place niche breadths respectively, and indicate similar or slightly narrower food niches in northern than southern populations for all but one of the five widely ranging species. Figure 11 graphs Horn's (1966) measure of overlap, R_o, for food and microhabitat overlap of each species with *Cnemidophorus* in northern and southern lizard assemblages. The arrows indicate changes in overlap from north to south for the four widely ranging species. Only one competitor (*Crotaphytus wislizenii*) shows a substantially decreased amount of overlap in the south, due to its becoming a more specialized feeder. In the southern parts of its range, *Crotaphytus wislizenii* eats 86% lizards (by volume), including *Cnemidophorus tigris,* whereas on northern areas lizard food comprises only 21% of the diet by volume (data and discussion in Pianka 1965). Thus the one species having distinctly less food overlap with *Cnemidophorus* accomplishes this by becoming its predator.

Data presented elsewhere (Pianka 1967) suggest that there is greater competition for food in both carnivorous and insectivorous bird species in the southern deserts. To the extent that their diets overlap, there should also be heightened competition between birds and lizards.

While the preceding is of necessity inconclusive, there is sufficient data to suggest that if competition varies with latitude, it is likely to be greater in the south.

CONCLUSIONS

A multitude of ecological differences exist between northern and southern populations of *Cnemidophorus tigris*. Southern populations have more predators, longer seasonal periods of activity, earlier maturation, smaller clutch sizes but more of them, and seem to have more competitors. The greater predation but smaller clutches characteristic of southern lizards is possible only because the longer seasonal period of activity in the south allows multiple breeding. At least two clutches are laid annually in the southern deserts, while northern lizards probably never lay more than a single clutch per year. Most members of northern populations aestivate during midsummer, probably because of the great daily range in temperature during that season. In addition, they must emerge from hibernation later than southern lizards, and hence have a considerably shorter period of seasonal activity. The ecological challenges facing the northern populations of this lizard are primarily generated by the physical environment, whereas the biotic components are relatively more important to southern populations. Tinkle (1969a) has reached similar conclusions in his studies on *Uta stansburiana*.

ACKNOWLEDGMENTS

I am especially indebted to my hard-working field assistants: Nicholas Pianka, William Shaneyfelt and Michael Thomas. Michael Pianka generously assisted in processing some of the data. Virginia Johnson assisted in many ways. I am grateful to Vera May Shirley for repeated careful typing of the manuscript. T. H. Frazzetta, M. F. Willson, H. S. Horn, R. T. Paine, G. H. Orians, C. C. Smith, H. F. Recher, R. C. Snyder, and R. H. MacArthur provided inspiring discussions and advice. My major professor, R. C. Snyder, gave his continuing encouragement and support. My wife, Helen, continues to be my most valuable critic.

Computer centers at the University of Washington (Seattle), Princeton University (Princeton), and The University of Texas (Austin) provided the use of their facilities and computer time.

It is a pleasure to acknowledge the financial support of the Department of Zoology at the University of Washington, the National Institutes of Health and the National Science Foundation.

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