ON LIZARD SPECIES DIVERSITY: NORTH AMERICAN FLATLAND DESERTS

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Abstract. Eight potential mechanisms for the determination of species diversity are described and discussed, and data relevant to each are presented for a particular diversity gradient: namely that of the flatland desert lizards of western North America. It is concluded that ecological time, spatial heterogeneity, length of growing season, and amount of warm season productivity are all factors which determine the total number of lizard species occurring on an area, but that the most important single factor is the spatial heterogeneity (mainly vegetative) of the environment. It is suggested that climatic variability allows the coexistence of many different plant life forms, the variety of which in turn controls the number of lizard species.

INTRODUCTION

The fact that there are usually more species of plants and animals in the tropics than in temperate regions has been recognized for nearly a century. A few groups appear not to follow this general pattern, but most major taxa are represented by more species at lower latitudes. The nearly universal occurrence of the phenomenon makes it likely that there is some general explanation underlying latitudinal differences in numbers of species, and this possibility has intrigued biologists for many years.

Description of differences in the total number of species occurring in different areas has given rise to the concept of "species diversity." Definitions of diversity always include the number of coexisting species (with diversity increasing as more species are added), and often incorporate as well the relative abundances of the component species (with diversity increasing as they become more equitably abundant). Thus species diversity is high when there are a large number of equally abundant species. Many different measures of diversity have been proposed and used (for reviews see Margalef 1958, MacArthur 1965).

Because of the global scale of latitudinal gradients in species diversity, there has been relatively little ecological investigation contrasting tropical with temperate diversity. (A fair number of these gradients have recently been described

(Fischer 1960, Simpson 1964, Terent'ev 1963). However, despite the paucity of pertinent ecological data, there has been considerable speculation as to the possible causes of diversity gradients (for reviews see Connell and Orias 1964, MacArthur 1965, and Pianka 1966). These efforts have produced at least eight different theories as to possible mechanisms for the control of diversity, which may be variously interrelated: (1) the evolutionary time theory, (2) the ecological time theory, (3) the theory of climatic stability, (4) the theory of spatial heterogeneity, (5) the productivity hypothesis, (6) the stability of primary production hypothesis, (7) the competition hypothesis, and (8) the predation hypothesis (Pianka 1966). A variety of causal sequences have been suggested which merge these mechanisms in different ways (Connell and Orias 1964, Paine 1966). For instance, climatic stability could determine both productivity and vegetative spatial heterogeneity, which in turn could regulate animal species diversity by means of either competition or predation. Such causal schemes may in fact control diversity, but their elucidation and substantiation must proceed by analyzing each link in the causal chain separately. Because many of these mechanisms could act in parallel or in series to determine any particular diversity gradient, separating and distinguishing between the different hypotheses is difficult. However, various predictions derived from the hypotheses allow most of them to be examined, and their probable importance assessed, along local diversity gradients.

It should be possible to elucidate the complete causal chain resulting in any particular diversity gradient when enough is known about the physical and biotic changes occurring along that gradient. Exactly analogous considerations apply to the determination of diversity ‖at any particular point, but usually investigation must proceed by comparison of several sites along a diversity gradient.

Whether or not local diversity patterns are determined by the same factors responsible for the latitudinal trends remains to be seen, but even if they are found to be controlled by different factors, thorough knowledge of the factors influencing local diversity will be necessary before latitudinal diversity gradients can be completely understood. In any case, it is a reasonable assumption that the two phenomena are closely related, and that there will be some sort of parallel between small and large scale systems. The present study of a particular diversity gradient, that of the flatland desert lizards of western North America, was undertaken to attempt to assess the importance of the various factors influencing diversity.

The Study System

The deserts of western North America form a continuous and enclosed series, uninterrupted by major physical barriers, over a latitudinal range of 1,500 mi, from southern Idaho and Oregon through Sonora and Baja California, Mexico (Shreve 1942). Three distinct regions within the series are recognized: a northern Great Basin, southern Sonoran desert, and an intermediate region called the Mojave desert. Because of their simplicity, deserts are especially suitable for synecological studies; the flatland desert has the added advantages of homogeneity, continuity, and extensiveness, and was therefore selected as a habitat type well suited for the investigation of species diversity. A series of ten flatland desert study areas, spaced out over about 10° of latitude (about 700 miles) was selected for study. These sites range from the Great Basin through the Mojave and Sonoran deserts (for exact locations and more detail see Pianka 1965). Each area was visited between 3 and 10 times during the season and quantitative data were taken on the reptiles, birds, and mammals present. In addition, 32 to 48 large quadrats (from 58 m² to 231 m²) were staked out on each area, and the perennial plants within these quadrats identified, measured and counted. Linear measurements were made of the height and width of the larger shrubs and trees, and their volumes estimated from the formula for the volume of oblate spheroids [$V = 4/3\pi ab^2$, where a is the linear dimension of the major axis (width), and b the same for the minor axis (height)]. No allowance was made for foliage density differences between shrub individuals or species. The records of the U.S. Weather Bureau stations closest to each site (and at similar elevations) were used to obtain climatological data.

Deserts are characterized by their low rainfall, and primary production has repeatedly been shown to be strongly positively correlated with precipitation (for African deserts Walter 1939, 1955, 1964; and for North American deserts Blaisdell 1958, and Pearson 1965). This strong correlation almost certainly has a causal basis, in that, because of its shortage, water probably acts as a "master limiting factor" on desert plants. The importance of these findings to the present study is that they allow crude estimation of the short-term, long-term, and variability of primary productivity on each study area (from the appropriate precipitation parameters). Abundances of desert animals vary seasonally and from year to year, depending especially upon the amount of recent precipitation. Also, because many desert lizard species are regular, but regularly rare occurrents in the flatland desert community, the simplest index of diversity—namely the number of species coexisting together in the same habitat—will be used to quantify lizard species diversity.

Four lizard species are found ubiquitously throughout the entire desert region (*Cnemidophorus tigris, Uta stansburiana, Crotaphytus wislizeni,* and *Phrynosoma platyrhinos*), and another 8 species (*Callisaurus draconoides, Sceloporus magister, Urosaurus graciosus, Dipsosaurus dorsalis, Uma scoparia, Coleonyx variegatus, Xantusia vigilis,* and *Heloderma suspectum*) are added variously in the southern deserts, never exceeding ten species on any given area. Figure 1 shows a contour map of the number of species of flatland desert lizards (based on range maps of Stebbins 1954). Quadrats 30 miles on a side were used in the construction of this map, which includes only 11 of the 12 species. [*Uma* was omitted because its range is much more restricted than Stebbins' map indicates (Norris 1958), and because it seems never to be found ecologically sympatric with *Sceloporus,* which is included on the contour map. The eleven species isopleth, located around the Boulder Dam region, was also omitted, as it appeared to be an artifact due to generally poorly known ranges, the extreme topographic relief of the area, and the quadrate method of constructing the map.]

All study areas are located on gently sloping bajadas, with contour intervals of 50 to 80 ft/mi, and cover from 6 to 20 mi² of continuous flatland desert. Usually my studies were restricted to a
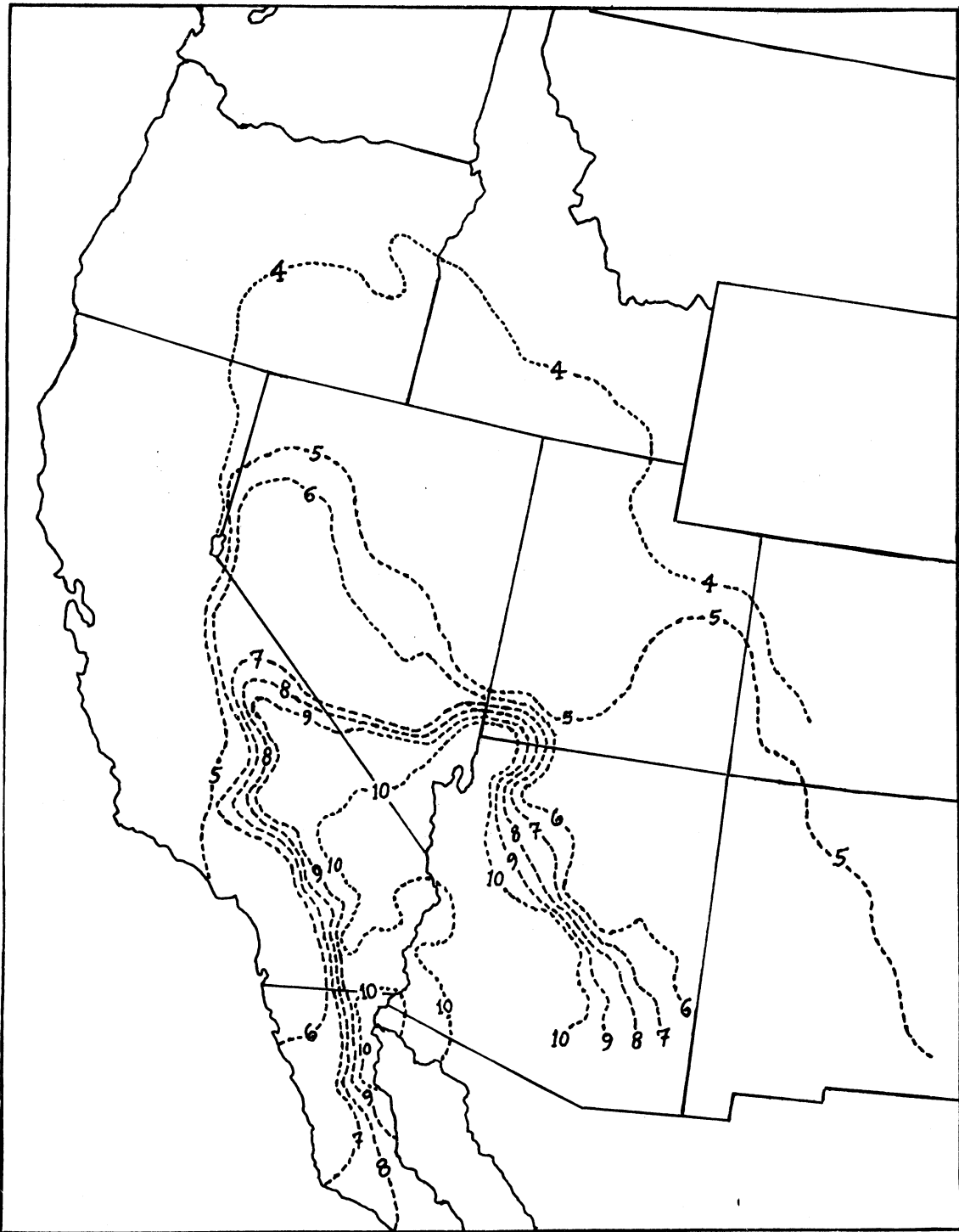
FIG. 1. Contour map of the number of species of flatland desert lizards, based upon eleven of the twelve species. The eleven species isopleth has been omitted (see text, adapted from range maps given by Stebbins 1954).

TABLE 1. Lizard species occurring on each of the study areas (numbers in parentheses are the total number of species known to occur on the area). U_1, U_2, and U_3 are the three areas reported on by Fautin (1946) from western Utah. The A- and E-areas were not as thoroughly sampled as were the other areas

Site	Total No. of species	Cnemidophorus tigris	Uta stansburiana	Crotaphytus wislizeni	Phrynosoma platyrhinos	Callisaurus draconoides	Coleonyx variegatus	Dipsosaurus dorsalis	Sceloporus magister	Urosaurus graciosus	Uma scoparia	Heloderma suspectum	Xantusia vigilis
U_1	(4)	×	×	×	×								
U_2	(5)	×	×	×	×								
U_3	(4)	×	×	×	×								
I	(4)	×	×	×	×								
L	(5)	×	×	×	×	×							
G	(5)	×	×	×	×	×	×						
V	(6)	×	×	×	×	×	×						
S	(6)	×	×	×	×	×	×						
A	(6)	a	×	×	b	×	?						
E	(6)	×	×	×	×	×	?						
P	(7)	×	×	×	×	×	×	×					
M	(8)	×	×	×	×	×	×	×		×			×
T	(9)	×	×	×	×	×	×	×	×		×	×	
W	(9)	×	×	×	×	×	×	×	×	×		?	
C	(10)	×	×	×	×	×	×	×	×	×			×

(For U_2 and U_3: plus Sceloporus graciosus an arboreal species)

a Cnemidophorus labialis
b Phrynosoma coronatum

few square miles, but on three more thoroughly sampled areas they were extended to about 6 to 10 mi^2. Table 1 gives the species composition and the total number of lizard species known to occur on each of the 10 areas. These numbers are very reliable, as many man-hours of lizard hunting were spent on each area, over the entire seasonal period of activity, and during the night as well as the daylight hours.

This study is based upon four seasons of field work; a total of 15 months were spent in the deserts, during which time over 8,000 lizards were observed (and over 4,000 collected). Only a small fragment of the data gathered can be presented here.

The assumption of normality is not justified for most of the correlations to be discussed, and thus the non-parametric Spearman rank correlation coefficient (symbol r_s) will be employed. Calculation and significance of this statistic follows Snedecor (1956) and Siegel (1956). Parametric statistics and tests were calculated from formulas and tables in Fisher (1958) and Fisher and Yates (1963). Standard symbols are used for the mean ($\bar{x}$) and standard deviation (s) in the text and tables.

EVOLUTIONARY TIME

Proponents of evolutionary time theory assume that community diversity (variously defined) increases with the age of the community. From this premise, it is argued that temperate communities are impoverished because of the recent glaciations and/or other disturbances, whereas tropical communities are "biotically mature" and hence more diverse. Thus it is often stated that there has not been time enough for speciation and evolutionary saturation (of number of species) in temperate regions; temperate species have not had long enough to adapt to, and completely occupy, their environment (Fischer 1960). This argument does not necessarily imply that temperate communities are ecologically unsaturated (that some of the resources are not being utilized), since a small component of species may, by expanding their individual habitat tolerances, use most or all of the available resources (Crowell 1962, MacArthur, Recher, and Cody, 1966).

The evolutionary time theory is very difficult to test because it involves such long time spans, and because there are no possible manipulations of the system. However, despite the difficulties of appraising the theory, some tentative conclusions have been drawn. Simpson (1964) has suggested several indirect tests, and has given reasons why the evolutionary time theory fails to explain mammal species density in North America. Several other workers (Connell and Orias 1964, Newell 1962) have argued that temperate species have had as long to adapt as have species in the non-glaciated areas. However, MacArthur (1965) argues that "it is possible that the pattern of the total number of species may be best given an historical answer, while the within-habitat patterns of diversity may have an equilibrium explanation." He asserts that the number of species within a given habitat reaches saturation fairly quickly, but that the total number of species may be continually increased by finer and finer habitat segregation (between-habitat diversity).

The paleobotanical studies of Axelrod (1950, 1958) on the evolution of desert vegetation provide a convenient, although perhaps somewhat oversimplified and diagrammatic outline of the history of the North American deserts. The major criticism of Axelrod's work is the undue emphasis on the somewhat artificial categories, "Madro-Tertiary" and "Arcto-Tertiary Geofloras" (Martin and Mehringer 1965). His general scheme is however a useful description and his dating and chronology are considered reasonably accurate. The primary assumption of the paleobotanist is that fossil plants related to, or similar to, modern plants had similar climatic tolerances and in general required comparable habitats. Most paleobotanists have used many different plant species simultaneously in assessing the climates and habitats of the past, thus effectively "averaging out" errors made due to physiological changes in some of the component species or taxa.

So called "subdesert" conditions prevailed in the general region of the present deserts for about 10 million years before the origin of true deserts. The first true desert conditions, as indicated by desert plant fossils, date from about 4 or 5 million years ago, but did not become widespread until about 425,000 to 600,000 years ago. There were two major regions by the latter time: a southern Mohavia and a northern Great Basin. The former included the area covered by the present day Mojave, Colorado, and Sonoran deserts; the latter corresponded roughly to the present day Great Basin. The warmer Mohavia had a more tropical flora and climate than that of the colder Great Basin. About middle Pleistocene (180,000 to 425,000 years ago), the northwestern part of Mohavia was uplifted, resulting in a cooler climate, changed precipitation pattern, and the loss of certain plants which persisted in the warmer Colorado and Sonoran desert portion of Mohavia. Some Great Basin ("Arcto-Tertiary") plants became established in the Mojave desert portion of Mohavia, gradually distinguishing the uplifted region from the present day Colorado and Sonoran deserts. Divergent development of the Mojave and Sonoran deserts continues today, as evidenced by remnants of the Mohavian ("Madro-Tertiary") flora apparently still retreating from the Mojave desert (Axelrod 1950, 1958).

Axelrod (1949) has published maps showing the approximate extents of the two floras during the Oligocene, Miocene, and Pliocene epochs. Martin and Mehringer (1965) give maps showing the distribution of desert and sagebrush vegetation during the full-glacial of the Pleistocene. In general, deserts expanded during the upper Tertiary, and then, with the onset of glaciation in the Pleistocene, became restricted to northern Mexico and the extreme southwestern United States. In the absence of fossils, there is no sure way of determining whether or not any of the twelve lizard species were present in the Great Basin during the Miocene and Pliocene. However, some educated guesses are possible from our knowledge of fossil plants and animals and thus the probable climate of the Great Basin during the upper Tertiary.

The occurrence of grazing mammals and the paleobotanical history indicate increasing aridity during the Tertiary and have been suggested as being indicative of the widespread development of grassland conditions during the middle Pliocene (Merriam and Sinclair 1907). Another indication of the development of grassland during this period is the evidence for rapid evolution of herbs and grasses in the Great Basin (Elias 1942; Stebbins 1947). The lizard species *Cnemidophorus, Uta, Crotaphytus,* and *Sceloporus* occur widely today in grassland areas surrounding the desert series, and the progenitors of these species may be presumed to have inhabited the Great Basin by the middle Pliocene. Probably *Phrynosoma platyrhinos* was replaced by the ancestor of *Phrynosoma douglassi,* the horned lizard species which occurs in the grassland regions today. Another lizard which almost certainly occurred on and adjacent to the prairies of this period is *Sceloporus graciosus,* which occurs today at higher elevations throughout the Great Basin and on the borders of grassland habitats (Stebbins 1954). The Gila monster, *Heloderma,* ranged further north in the Oligocene, as evidenced by the fossil *Heloderma matthewi* from Colorado (Gilmore 1928), and it probably occurred in this general region during much of the upper Tertiary.

Thus, it is likely that at least seven lizard species have been associated with cold desert conditions (Great Basin desert) since the origin of sub-desert conditions during the Pliocene. Because sub-desert and true deserts came into existence at about the same time in both the north and the south, it follows that lizards have been evolving in "cold" deserts nearly as long as they have been associated with "warm" desert conditions. If this is true, lizards have had as long to adapt in both types of desert. However, it is probable that more species have been associated all along with the southern warmer deserts than have been evolving in association with the northern colder deserts. Therefore, it is unfortunately very difficult to make any definitive statements about, or to assess the influence of evolutionary time upon, the evolutionary history of the desert lizard species diversity gradient.

ECOLOGICAL TIME

The ecological time theory deals with shorter time spans than the evolutionary time theory. Of paramount importance is the time required for dispersal of species into newly opened areas of suitable habitat (or remote areas), rather than the time necessary for the evolution of new species or for the adaptation of species already in existence. According to this theory, there has not been time enough for species to move into the temperate zones, and these areas are thus unsaturated in the total number of species they now support. (Again, such areas can still be ecologically saturated, if the species which have managed to populate them have large populations and broad habitat tolerances, thereby utilizing the full spread of useable resources.) Ecological time would seem to be an important determinant of diversity only in cases where there are pronounced barriers to dispersal. The theory of dispersal as a deter-

minant of diversity has been developed recently for islands by MacArthur and Wilson (1963).

There is reasonably good evidence that the majority of continental habitats are evolutionarily saturated with species, and that nearly all habitats are ecologically saturated with individuals (Elton 1958, MacArthur 1965). Both Crowell (1961) and MacArthur et al. (1966) have demonstrated that island bird species use more of the habitat space than do their continental counterparts, indicating some lability in habitat requirements, and that island habitats may well be ecologically saturated even though impoverished in terms of the total number of species present. Deevey (1949), MacPherson (1965), and Miller (1958) treat some cases where ecological time has been an important factor.

With regard to the desert lizard diversity gradient, there is good evidence that there has been time enough for lizards to disperse throughout the entire desert series. During the upper Pleistocene (the last 180,000 years) there were several floodings of all three deserts, especially of the Great Basin and Mojave deserts, with subsequent arid periods and reconstitution of desert conditions. Presumably deserts were never totally eliminated during these floodings, but persisted in local patches, which spread out when more arid conditions returned. Thus deserts were alternately contracted and expanded during the upper Pleistocene; the contractions corresponding roughly to the glacial maxima, and the expansions to the retreat of the glaciers. The three most recent pluvial periods in the Great Basin and Mojave deserts have been fairly accurately dated by radiocarbon chronology at 25,000–14,000 and about 11,700–11,000 years ago, with a much smaller third peak at about 10,000 years before the present (Broecker and Orr, 1958). The same data indicate low water levels during the past 9,000–10,000 years. The Colorado and Sonoran deserts were dry during the last pluvial period and have acted as a reservoir from which desert animals spread during the subsequent dry period (Banta 1961, 1962). Thus, there has been nearly 10,000 years for lizards to completely re-occupy the Great Basin desert. A rate of movement of only 60 m per year would suffice to disperse a species through the entire Great Basin in this amount of time. Since most lizard species are capable of moving this far in a few days, we may safely conclude that there has been ample time for reinvasion of the entire desert region, and that the 8 species which are restricted to the southern deserts are held there for ecological reasons, rather than for lack of time for dispersal. This is not strictly true, since one species (*Uma*) occupies a specific habitat (sand dunes) which is usually rather disjunct in space. Thus, *Uma* may actually not have had time enough to occupy all potentially suitable habitats. With this single exception, however, the flatland desert lizards of western North America would appear to have had ample time for dispersal.

In the Viscaino desert portion of the Sonoran desert in Baja California, *Callisaurus draconoides crinatus* appears to fill the ecological role of *Uma* in other regions (Norris 1958). The striking convergence in body form and habits has also been reported on by Mosauer (1932), and suggests that most of the extensive sand dune areas in the south support a *Uma* or its *Callisaurus* equivalent. However, this sand dune lizard type is completely lacking from the Great Basin desert, even though there are fairly extensive areas of loose sand. It is difficult to know whether or not *Uma* could exist in the Great Basin desert sand dune areas. The transplant of population innocula large enough for mating and reproduction to several appropriate sand dune areas further north might settle this question, and would be a fruitful enterprise whether or not positive results were obtained.

CLIMATIC STABILITY

Areas with stable climates should usually possess relatively constant supplies of the various resources important to plant and animal populations. The most important resources for plants are temperature, light, water, and nutrients; the first three are a direct function of climate, while the fourth (nutrients) may often be indirectly controlled by climate. Thus, it is reasoned, plant populations and plant activities are more constant in regions with stable climates than in areas with more erratic climatic regimens. Such stability of climate and vegetation, in turn, creates an unvarying environment for animal species, and allows them to successfully evolve restrictions on their habitat and food requirements. It is argued that increased food or habitat specialization results in increased overall efficiency, and is therefore advantageous up to the point where the benefits derived from increased specialization are outweighed by the disadvantages incurred (MacArthur and Pianka in press). The point at which this shift occurs increases with increased resource stability and/or predictability, and therefore with high climatic stability. Thus regions with stable climates allow the evolution of finer specializations and adaptations than do areas with more erratic climates, because of the relative constancy of resources (Klopfer 1959, MacArthur 1965). More species (each one rarer) can occupy the unit of habitat space, and "niches" are smaller in more

stable climates (Klopfer and MacArthur 1961). The mechanism suggested for the control of diversity by the theory of climatic stability can also apply to climatic predictability; thus, an area with a highly predictable, but variable annual climatic pattern could conceivably allow species to specialize on those resources which were predictable from year to year, thereby increasing diversity. Both the stability and the predictability of climate should therefore be examined for any given diversity gradient.

There is a latitudinal component to the thermal environment in the desert system, with progressive lowering of average monthly temperatures every month of the year as one proceeds northwards. Thus, the length of the frost-free period or the "growing season" becomes shorter the further north one goes. One of the first "explanations" for the fact of greater lizard species diversity in southern deserts than in the north which frequently comes to mind is "obviously, there are more lizards in the south because it is warmer there." However, the successful existence of five lizard species in northern deserts casts some doubt on this assertion; for if the lizard body plan can be successfully adapted to colder climates at all, why have not more species evolved or migrated into the northern deserts? Despite this objection there is a strong correlation between the number of lizard species and the mean July temperature (Fig. 2). Similar correlations were found for

bird, mammal, and reptile species numbers in the Soviet Union (Terent'ev 1963). No probable causal mechanism for this correlation is apparent and it is highly likely that an important intermediate factor has been omitted in making these correlations. The length of the frost-free period is highly correlated with mean July temperature in deserts, and appears to have more potential as a direct determinant of diversity than the latter. The frost-free period, or "growing season," may be considered to be a measure of the temporal heterogeneity or the "stability of primary production" on the area concerned. There is also a strong correlation between the number of lizard species and the average length of the frost-free period (Fig. 3). Thus, it is highly possible that

FIG. 3. The total number of lizard species plotted against the average length of the frost-free period or the "length of the growing season" (with one point from Fautin's (1946) data).

the correlation depicted by Figure 3 is the basis for the correlation shown in Figure 2 (the same causal sequence might apply to Terent'ev's results).

There are at least two possible causal mechanisms relating growing season with the number of lizard species: (1) there may be more possibilities for "niche" diversification in areas with longer average seasonal periods of lizard activity. Thus, the short growing season (about 110 to 140 days) in the northern deserts may not allow temporal partitioning of environmental resources, whereas the longer season (160 to 290 days) in the south might allow the component species to separate temporally their periods of activity (Ricklefs 1966). And (2), the longer season might allow some species to decrease their daily energy intake and successfully restrict the range of resources they utilize (i.e., become more "specialized"). Such specializations would tend to leave unused resources and presumably would make it easier
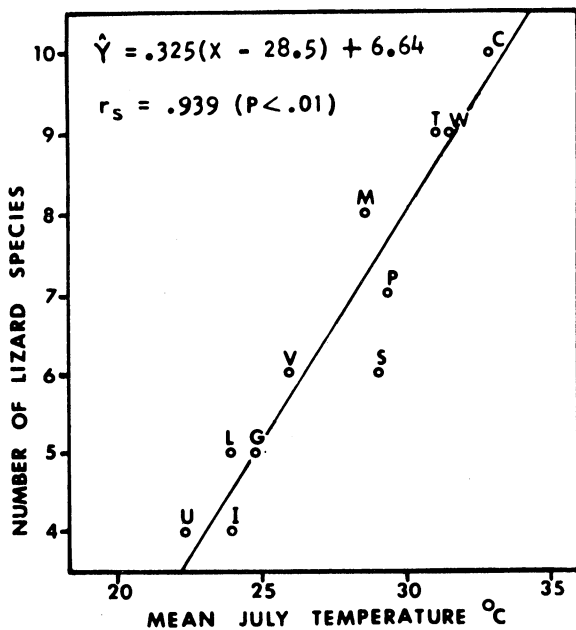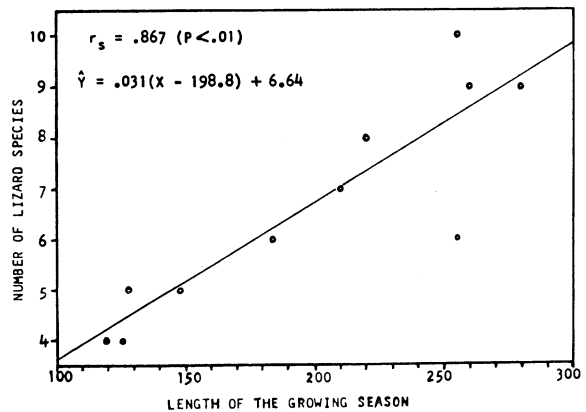

FIG. 2. The total number of lizard species plotted against the mean July temperature in degrees Centigrade. One point is taken from Fautin's (1946) data from western Utah.

for new species to establish themselves. One nocturnal species (*Coleonyx*) is probably directly dependent upon the longer frost-free period in the southern deserts, and the herbivorous species *Dipsosaurus* displays a strongly seasonal period of activity (Pianka 1965). The relations of other lizard species to the length of the growing season are less obvious and are probably indirect. For example, growing season might, by directly affecting plant life form diversity, indirectly control the number of lizard species.

Differences in the daily temperature regimens between deserts may be considered to be largely unimportant in determining the total number of lizard species, because the lizards compensate for them by both physiological and behavioral means. *Cnemidophorus* displays a cline in its average body temperature along the desert series, with significantly lower body temperatures in the northern deserts (Pianka 1965). Lizards also emerge later in the north, when ambient environmental temperatures are more comparable to those utilized by southern populations. Although the northern deserts are colder, the diurnal rate of change of temperature during the growing season is nearly parallel in all three deserts, the major difference being that the northern deserts warm up later, and never get as warm as the southern deserts (Fig. 4). Lizards are largely inactive during the very hot periods in all deserts, and extremely high temperatures can hardly be considered to improve conditions for them. The amount of time spent above ground feeding each day, if it differs latitudinally, is usually longer in the north (Pianka 1965). Thus, the portion of the day used by the lizards is thermally fairly uniform from north to south, and while it is not possible to refute rigorously the importance of thermal variability, it
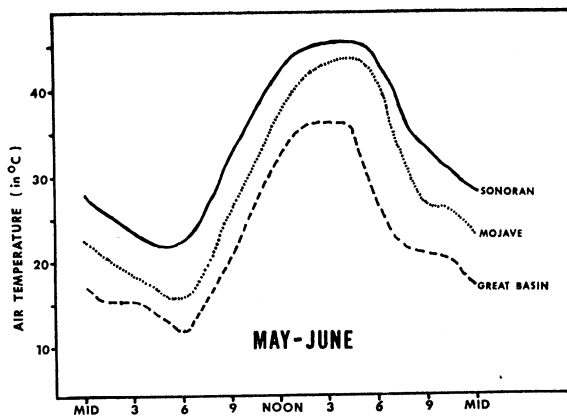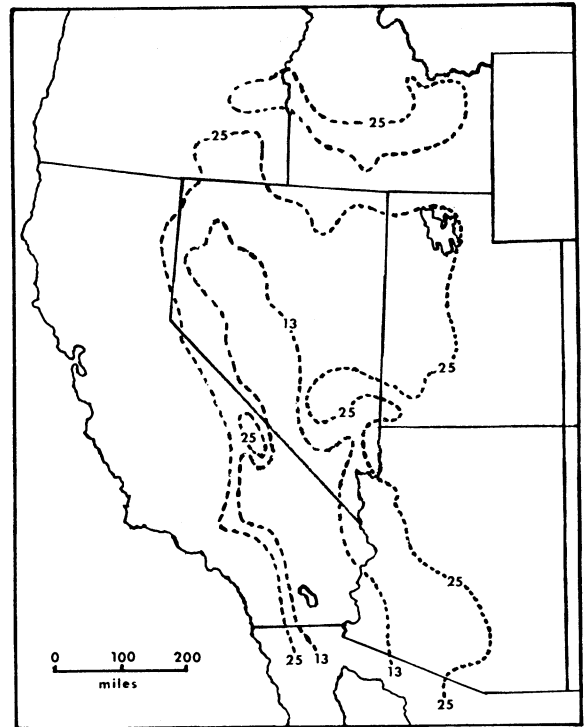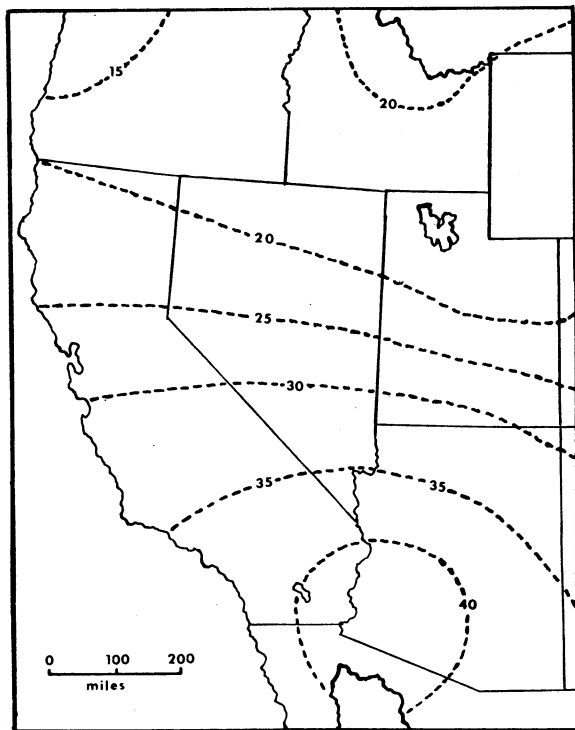

LONG-TERM AVE. ANNUAL PPTN. (13 & 25 Cm. isopleths)

Fig. 5. Isopleths of the long-term mean annual precipitation for the desert region. Only the 13 and 25 cm isopleths are shown (adapted from Anon., Climate and Man 1941, and Visher 1954).

seems likely that it is not an important factor controlling the ranges of these desert lizards.

Precipitation, the other primary component of climate, has a more complex pattern and distribution across the deserts, and is inherently more interesting because of the strong dependence of productivity upon water in desert regions (Walter 1939, 1964). Figure 5 shows isopleths for the long-term average annual precipitation in the desert series, and demonstrates that there is little latitudinal component to the average annual total precipitation. There is a longitudinal trend, however, with the inner deserts (Mojave and south-central Great Basin) receiving less water than the outer fringe of desert. There is generally an inverse relationship between the average amount of precipitation falling on an area and the variability of that precipitation, the distribution of the latter measure being shown in Figure 6. Variability of annual precipitation is greatest in the Mojave desert, intermediate in the Sonoran desert, and least in the Great Basin desert. Thus, on a yearly basis, the precipitational component of climate is more variable in the southern deserts than in the north, which fact is evidence against the theory of climatic stability.

Fig. 4. Actual diurnal changes in air temperature recorded at 3 of the 10 study areas; these data are representative of the spring–early summer daily march of temperature patterns in each desert type.

ANNUAL VARIABILITY OF PPTN. (% dev. L.T. MEAN)

FIG. 6. Isopleths of the annual variability of precipitation. The index of variability is the average percentage deviation from the long-term mean precipitation (see text, adapted from Finch and Trewartha, 1949).

There are distinct patterns of rainfall during the year in different portions of the desert series, and it is necessary to examine monthly as well as total annual rainfall. Such an analysis showed monthly patterns of variability of precipitation generally similar to that already elaborated for total annual precipitation. Because the variability of precipitation varies directly with the number of lizard species, rather than inversely as predicted by the theory of climatic stability, and because thermal variability appears to be unimportant to the lizards, it is tentatively concluded that climatic stability is not an important factor controlling this particular diversity gradient.

Variability is not the inverse of predictability, as it is possible to have a very predictable, yet still quite variable, pattern of rainfall from month to month. The statistical technique of time-series analysis or "autocorrelation" allows quantification of predictability even in cases with variable patterns. Monthly precipitation records were used in the following analysis, which is based upon from 50 to 80 years of nearly continuous monitoring of precipitation by the U.S. Weather Bureau (U.S. Weather Bureau Bulletin W, 1930, and Supplement, 1952; Climatological Data, 1953–

1964). Autocovariance is positive when values of x are positively correlated with values of x at an earlier time, and negative when the two values are inversely correlated. Values near zero indicate independence of the two x-values, and thus also indicate unpredictability. The lag was allowed to vary from zero (no lag) to 36 months, but autocorrelation was found to follow an annual cycle, repeating, in amplitude and periodicity, the pattern seen during the first 12 lag periods, when the lags were made longer.

Figure 7 graphically illustrates the autocovariance calculations for lag periods from zero to 12 months, showing that the Great Basin has the least predictable precipitational regimen, and that the Mojave and Sonoran deserts have distinctly different and more predictable patterns of monthly rainfall. Thus the Sonoran desert shows a six-month periodicity, with inverse predictability at lags of 2–4 and 8–10 months, but positive predictability at longer lags of 5–7 and 11–12 months. The Mojave desert displays a 12-month periodicity, with negative autocorrelations at lags of 4–8 months and positive ones from 0–3 and 9–12 months. Figure 7 illustrates the annual march of average monthly precipitation, and shows clearly the biennial pattern of rainfall of the Sonoran desert (both winter and summer rains), the single period of rain in the Mojave desert (winter rain), and the near absence of periodicity in rainfall of the Great Basin desert.

The lag period important for the continued existence of most lizards is almost certainly longer than that for animals with shorter life spans and/ or higher metabolic rates, such as insects and birds (R. H. MacArthur, pers. comm.) ; however, not enough is known to predict the critical lag period for any group, and it is difficult to evaluate Figure 7 in terms of the associated lizard faunas, except in a rather qualitative way. It is certain that the average duration of drought will be shorter in the Sonoran than in the Mojave desert due to the longer periodicity of the Mojave, but the near lack of periodicity in Great Basin precipitation makes it difficult to judge the harshness of conditions there for the lizards. The inverse predictability (at 4–8 months lag) characteristic of the Mojave desert is a reflection of the winter-wet, summer-dry conditions, and does not mean that conditions are good for the lizards. Although the pattern of rainfall is determinant, there is seldom any rain when the lizards are active, and it is likely that conditions are actually harshest (for the lizards) on the Mojave, intermediate in the Great Basin, and best in the Sonoran desert. Because 11 of the 12 lizard species occur in the Mojave desert, it is reasoned that climatic predictability is not an im-

Points above the zero line indicate positive autocorrelation, and mean that the precipitation for a given month is positively correlated with the precipitation for the months at a given lag period away. Points below the zero line are indicative of inverse autocorrelation, meaning that conditions may be expected to change by the next lag period (i.e., given a six month lag, if it is wet in January, it is probable that it will be dry in June, and vice versa). Points near the zero line indicate that there is little autocorrelation, and that precipitation is random and unpredictable.
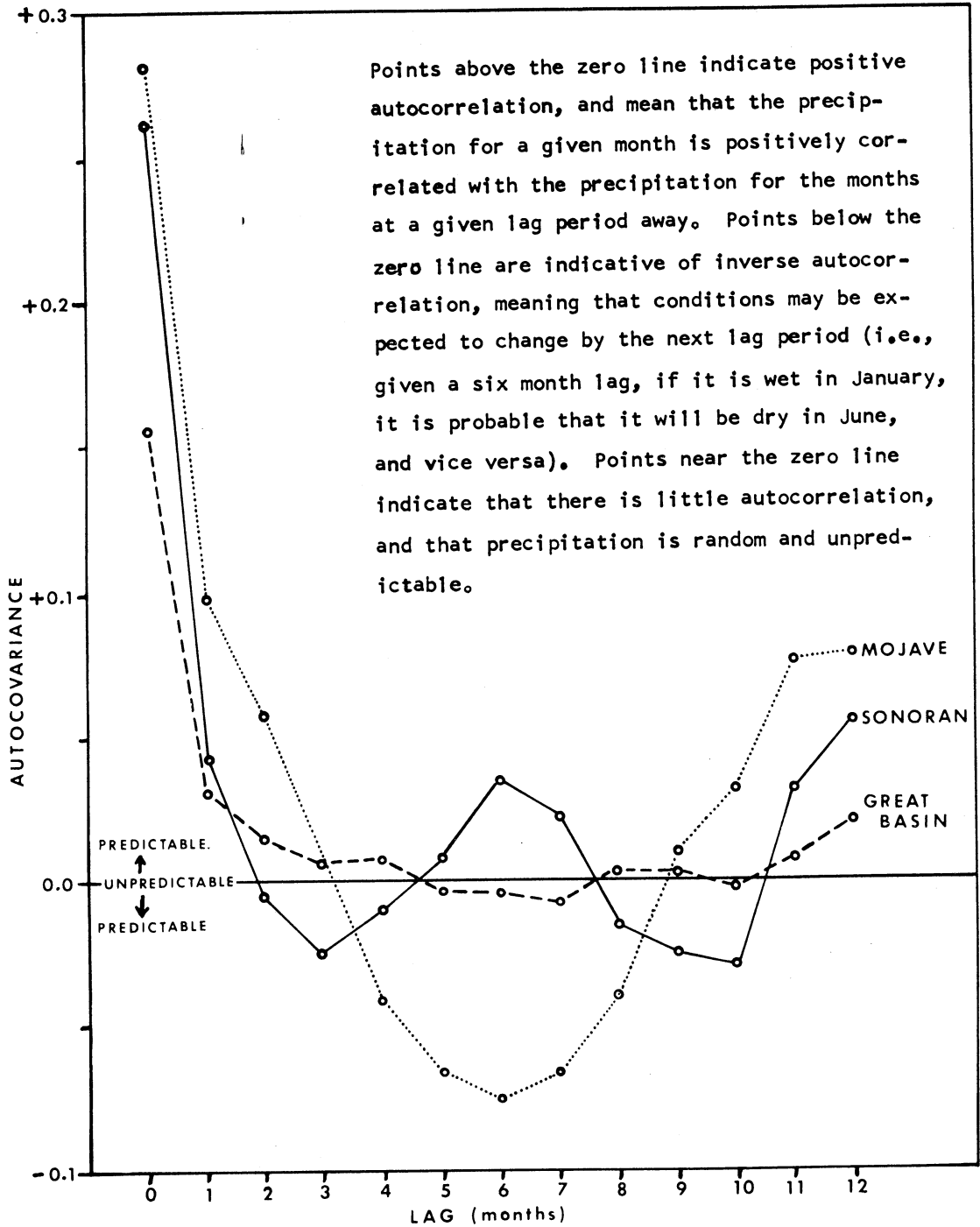
FIG. 7. Autocovariances of monthly total precipitation data, for lags of 0 to 12 months. Values shown are for 3 of the study areas, and are typical patterns for each desert type (each line is based upon between 600 and 1,000 monthly rainfall totals).

portant factor allowing the coexistence of lizard species.

SPATIAL HETEROGENEITY

More complex habitats should, everything else being equal, support more species of plants and animals since each of the species can live on or in a different part of the environmental mosaic. Spatial heterogeneity has been investigated at two levels, that of macro- and micro-spatial heterogeneity (Pianka 1966). The first is discussed by

Simpson (1964) as topographic relief. That topographically diverse areas possess more habitats (and thus more species) than topographically simple areas is a tautology: more habitats exist in tropical topographically diverse regions than in temperate ones, which lack the true tropical habitats (Pianka, 1966). Thus, gross geographic lumping of habitats includes both within- and between-habitat diversity (MacArthur 1965, Simpson 1964). The first kind of diversity is of special interest to ecologists and is the primary concern of the present investigation.

There are several components to micro-spatial complexity, including horizontal, vertical, and qualitative heterogeneity of both the physical and biotic elements in the environmental mosaic. The fact that vertical vegetative spatial complexity controls bird species diversity has now been well documented (MacArthur and MacArthur 1961, MacArthur, MacArthur, and Preer 1962, MacArthur 1964, 1965, MacArthur et al. 1966). The importance of spatial heterogeneity of physical elements in the environmental mosaic has not yet been adequately studied, but may prove to be causally correlated with animal diversity in some soil and infauna communities (Hairston 1959, and Lie, pers. comm.).

I have reported upon the relationship between the lizards and the spatial heterogeneity of the habitat elsewhere (Pianka in press), and will only outline those findings briefly here. There are strong latitudinal changes in both the vertical and horizonal components of vegetative spatial heterogeneity along the desert series of western North America, with spatial heterogeneity of both types being greater in the southern deserts than in the northern ones (Shreve 1942, 1951). Small

semi-shrub species occur throughout the entire region. The Sonoran is an arboreal desert with several species of trees and many large woody shrubs, the Mojave supports the large woody shrub *Larrea divaricata* and a few *Yucca brevifolia* "trees," and the Great Basin is structurally a very simple desert with predominantly a single perennial plant life form (low semi-shrubs). The small shrubs in the northern deserts are usually very densely packed and uniformly spaced, so that horizontal spatial heterogeneity is low, whereas the addition of perennial life forms in the southern deserts is often accompanied by fewer plant individuals per unit area and greater horizontal heterogeneity in their distribution in space.

The horizontal component of vegetative spatial heterogeneity may be estimated by the between quadrat variability in percentage cover and standing crop (Table 2). The number of lizard species is significantly positively correlated with both of these measures, indicating that there may be a dependence. In order to quantify the vertical component of spatial heterogeneity, three plant volume categories were selected corresponding to the three natural vegetative layers: (1) the small semi-shrubs under 0.7 m³, (2) the larger woody perennials between 0.7 m³ and 22.0 m³ (mainly *Larrea divaricata*), and (3) the largest shrubs and trees over 22.0 m³ (methods of calculating volumes have been given previously in this paper). The proportion of the total number of perennials falling into each of these three categories were used as p_i's to compute "plant volume diversities" according to the information theory formula

$$H = - \Sigma p_i \log_e p_i$$

of Shannon (1948). Plant volume diversity was

TABLE 2. Summary of perennial plant data (quadrat size = 230.7 m²)

| Site	Number per quadrat		Estimated Standing Crop (per quadrat) volume in cubic meters		Estimated Coverage in % of total surface		Plant Species Diversity	Plant Volume Diversity
	$\bar{x}$	S	$\bar{x}$	S	$\bar{x}$	S		
U₁	401.1	—	—	—	20.2	—	1.32	—
U₂	351.4	—	—	—	21.6	—	1.37	—
U₃	637.0	—	—	—	8.0	—	1.55	—
I	~349	—	—	—	~20	—	1.76	—
L	222.4	33.6	16.1	0.9	6.0	1.2	0.80	0.08
G	307.4	39.3	49.4	1.4	14.8	2.0	1.46	0.13
V	109.7	31.3	74.3	1.6	10.8	2.2	1.24	0.36
P	72.9	22.5	55.5	1.5	9.1	2.1	0.91	0.25
S	161.2	21.9	54.1	2.4	10.3	3.4	1.24	0.41
A	77.8	—	—	—	~6	—	0.57	0.02
E	42.5	—	—	—	~10	—	1.09	0.54
M	83.0	24.0	142.7	2.3	13.3	3.3	1.73	0.44
T	14.3	5.2	90.9	2.5	9.1	3.6	1.14	0.82
W	33.6	16.8	77.4	4.1	9.3	5.7	1.23	0.62
C	40.0	19.6	73.1	6.4	10.5	9.0	1.36	0.53
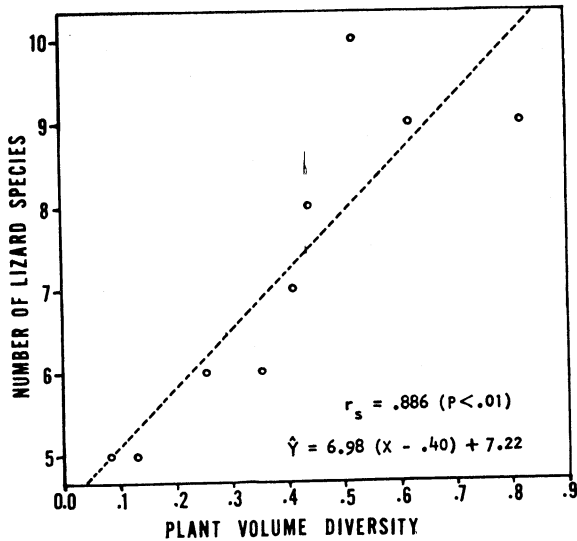
FIG. 8. The number of lizard species plotted against the diversity of perennial plant volumes irrespective of plant species. P.V.D. is based on 3 volume categories, approximately equivalent to small shrubs, large woody shrubs, and trees (see text).

found to be more strongly correlated with the number of lizard species than either of the horizontal measurements of spatial heterogeneity, and is illustrated in Figure 8.

An accurate index of the qualitative component of heterogeneity is impossible without a priori knowledge of which elements of the environmental mosaic are important to the lizards. However, the vegetative aspects of qualitative heterogeneity may be estimated from the same formula and the relative abundances of each of the shrub species. The proportion of the total number of plants represented by each of i species were used as p_i's in Shannon's formula to compute "plant species diversities." There is no correlation between this index and the number of lizard species (Table II), indicating that vegetative qualitative heterogeneity, per se, is of minor importance in controlling lizard species diversity.

Because there are very few structurally simple southern flatland deserts and no complex arboreal northern desert regions, it is difficult to vary spatial heterogeneity independently of latitude. However, three areas examined in the present study provide interesting exceptions: (1) the S-area, at the southernmost tip of Nevada on the boundary of the Mojave and Sonoran deserts, supports no trees and only very small stunted *Larrea* bushes; this site has a long growing season, but a low plant volume diversity, and supports only six lizard species. (2) The E-area in the Mojave desert completely lacks *Larrea* and supports only a few large woody perennials, but

has a long growing season (about 245 days), and the same six lizard species as the S-area. (3) Although inadequately studied, an area containing only low semi-shrubs in Baja California supports *Uta, Crotaphytus, Callisaurus, Cnemidophorus labialis,* and *Phrynosoma coronatum* (5 species), and may also have *Coleonyx*. This very simple site is at latitude 28°, but no data are available on growing season.

Further strong support for the importance of spatial heterogeneity as a determinant of the number of lizard species is found in the autecologies of the component species (Pianka 1965, in press). Lizards partition the environmental mosaic spatially and have specific micro-habitat preferences and preferred modes of foraging.

PRODUCTIVITY

According to the productivity hypothesis, greater production results in greater diversity (all else remaining equal) by way of two mechanisms: (1) a resource which is too sparse, in an unproductive habitat, to allow a species using it to replace itself, will support that species in a more productive habitat because there is more of the resource (MacArthur 1965), and (2) if the spread of useable resources remains the same, but each resource type is more plentiful in a more productive habitat, the species using these resources can decrease their search time and thus increase their efficiency by restricting themselves to a smaller range of the useable resources (MacArthur and Pianka in press). Therefore more species can coexist, each one using less of the variety of environmental resources, in a more productive habitat. Thus, the compromise between specialization and generalization resulting in maximal foraging and reproductive efficiency is seen to shift with productivity, similarly to the way in which this compromise is supposed to shift with resource stability (see section on climatic stability). Aspects of the productivity hypothesis have been discussed by Connell and Orias (1964), MacArthur (1965), MacArthur and Pianka (in press), Paine (1966), and Pianka (1966).

Figure 5 shows isopleths of the average annual precipitation for the desert region, which, because of the strong correlation with productivity, may be considered to indicate the amount of primary production in different parts of the desert series. Even a hasty comparison of Figures 1 and 5 suffices to show that there is little relation between the number of lizard species and the average annual precipitation. There is, however, a loose positive correlation ($r_s = .586$, $P < .05$) between the average annual precipitation and lizard abundance (all species combined); and this correlation

is improved if the average precipitation for the past five years is used. Table 3 gives some precipitation parameters calculated from U.S. Weather Bureau data for each of the study areas and for the area reported upon by Fautin (1946). The correlation between long-term average annual precipitation and the number of lizard species is insignificant ($r_s = .105$), as is the correlation between the total precipitation during the year prior to study and the number of lizard species ($r_s = -.069$). Because a substantial portion of the annual precipitation falls during the winter months, and at least some of the subsequent production is therefore probably not available to the lizards, it is desirable to examine also the average warm season precipitation for latitudinal trends (Table 3). The average amount of precipitation during the frost-free period or "growing season" is also not significantly correlated with the number of lizard species ($r_s = .397$), and there would appear to be little relation between productivity and species diversity of these desert lizards.

STABILITY OF PRIMARY PRODUCTION

Much of the theoretical argument for the stability of primary production hypothesis has already been presented under the theory of climatic stability, as the 2 are intimately related and inevitably part of the same causal sequence. However, plants may sometimes buffer climatic variability (and/or predictability) by utilizing their own homeostatic adaptations and storage capacities to increase the stability of primary production and thereby the diversity of the community. Also, there is evidence that many plants actually store the products of their primary production, expending this stored energy in one great bloom of flowering and seeding, and thus actually reduce the stability of the system (Garman 1955, Keen 1958, Smith 1965). (This procedure periodically reduces predator populations, and maximizes the plant species' reproductive success.)

The longer growing season of tropical regions may allow the component species to partition the environment temporally as well as spatially, and thereby permit the coexistence of more species (MacArthur 1964, Ricklefs 1966). Also, the smaller clutch sizes characteristic of tropical birds (Skutch 1954, 1960) may allow the coexistence of more species in the tropics; by reducing its clutch size, a species lowers its total energy requirements and is therefore able to survive in less productive areas which were formerly marginal habitats (note that this has the same effect as increased stability of primary production) (MacArthur 1965). Such reductions in total energy requirements would

also allow the existence of more species, if the total amount of energy available is constant (MacArthur 1965).

Although no direct data on primary production are available, there are several possible ways of attempting to examine the importance of this mechanism of control of diversity in the present diversity gradient: by means of the variability of precipitation (or production), the length of the frost-free period, and by lizard clutch size. In addition, the predictability of primary production may be reflected by the time-series analysis of precipitation and the pattern of autocovariance versus the lag period (Fig. 7). Each kind of relevant data will be examined and discussed, as they do not always lead to the same conclusions. (The possible reasons for such differences will be discussed at the end of this section.)

Variability of primary production should follow a trend parallel to that seen for the variability of precipitation (see section on climatic stability and Table 3). Although there is a weak positive correlation between the number of lizard species and the standard deviation in annual precipitation, it is not significant at the usual (.05) level of acceptance. Because the stability of primary production hypothesis predicts an inverse correlation, it must be rejected after consideration of the present data. The same conclusion is reached if monthly variability of precipitation is considered, although the data are more complex and the analysis correspondingly more difficult. Thus, the relation between the number of lizard species and the variability of primary production is, if anything, a positive one, with more species from areas with more variable production. It is even possible that lizards may capitalize on this variability and that it has been an important factor contributing to their relative success over birds in desert regions.

Growing season has been seen to be strongly correlated with the number of lizard species (see Fig. 3 and the section on climatic stability), but only one species (*Coleonyx*) appears to be directly dependent upon the longer frost-free period of the southern deserts.

Clutch size is smaller in the south in one species (*Cnemidophorus*), but is larger in two other species (*Uta* and *Crotaphytus*), and does not vary in the two remaining widely ranging species (*Phrynosoma* and *Callisaurus*) (Pianka 1965). Hence, reduced clutch size is not generally concomitant with more diverse desert lizard communities, and does not appear to be a factor allowing the coexistence of more lizard species in the south.

Examining now the predictability of warm-season primary production, as estimated by time-

TABLE 3. Summary of annual precipitation and various other precipitation parameters (in centimeters)

Study Site	Long-term parameters			Mean Percent Deviation	N	Short-term (last 5 years) mean pptn.		Nearest U.S. Weather Bureau Station (source of data)	Miles to Site	Mean Growing Season (days)	Long-term Mean warm Season Precipitation
	$\bar{x}_{lt}$	S	S/$\bar{x}$			1959–1963	1960–1964				
U	17.00	5.00	.294	23.3	42	17.53	(–1941)	Deseret, Utah	40	126	4.47
I	18.40	5.57	.303	36.4	43	20.19	(–1962)	Grand View, Idaho	25	120	3.51
L	13.96	5.52	.395	32.6	49		14.76	Lovelock, Nevada	4–5	128	3.26
G	9.60	4.36	.455	41.0	68		9.17	Mina Hawthorne, and Gabbs, Nevada	5–40	148	2.89
V	11.56	6.58	.569	54.2	45		9.91	Beatty, Nevada	25	184	2.81
P	9.34	5.88	.629	100.1	35		8.66	Lathrop Wells and Pahrump, Nevada, and Kingston, Cal.	15–40	210	3.48
S	18.70	10.47	.560	49.2	49		14.07	Searchlight, Nevada	10	255	10.47
M	12.73	9.21	.723	61.5	60	10.90	10.24	Mojave, California	5	220	1.25
T	9.40	6.12	.651	52.0	25	8.61	9.75	Twentynine Palms, Calif.	15	280	7.11
W	19.24	8.00	.416	35.2	50	12.87	12.09	Salome, Arizona	14	260	11.44
C	20.86	7.62	.365	42.3	44	18.49	19.38	Casa Grande, Arizona	10	255	13.10
E	11.99	—	—	38.2	14	—	—	Barstow, California	35	245	6.12

series analysis of precipitation (Fig. 7), it has been seen that the Sonoran desert is probably the most, the Great Basin next, and the Mojave definitely the least, predictable in having substantial warm-season precipitation. (Actually, the Mojave is most predictable in having very little warm-season production, due to the regular occurrence of the long summer drought.) Since 11 of the 12 lizard species occur in both the Mojave and Sonoran deserts, predictability of warm-season production is probably not an important factor regulating lizard species numbers. One species, however, is restricted to the Sonoran desert (*Heloderma*) and, because it is a secondary carnivore, is almost certainly dependent on the summer rains of the Sonoran desert, with their concomitant predictable burst of warm-season production and breeding of *Heloderma*'s prey species (Pianka 1965).

In summary, only one of the four possible measures of the "stability of primary production": the average length of the frost-free period, is significantly correlated with the number of lizard species and the causal chain resulting in this correlation is probably an indirect one. Further support of the indirect nature of this relationship comes from the fact that three other measures of the "stability of primary production," especially monthly and annual variability of precipitation, are not significantly correlated with the number of lizard species. Length of the growing season could directly affect plant life form diversity,

thereby indirectly regulating lizard species diversity (see also section on spatial heterogeneity), but this possible causal chain is speculative. Only the two nocturnal lizard species *Coleonyx* and *Heloderma* seem to be directly dependent upon the length of the growing season and the predictability of warm-season production, respectively.

COMPETITION

The competition hypothesis states that natural selection is largely controlled by the exigencies of the physical environment in the temperate zones, whereas biological competition (either intra- and/or inter-specific) is a more important determinant of the course of evolution in the tropics (Dobzhansky 1950, Williams 1964). Dobzhansky (1950) reasons that natural selection proceeds in a different direction in the tropics, because density-independent mortality factors, such as drought and cold, seldom occur there. He observes that catastrophic mortality usually causes selection for increased fecundity and/or accelerated development and reproduction, rather than selection for competitive abilities and interactions with other species. Tropical species will therefore be more highly evolved and possess finer adaptations than will temperate species, due to the more directed mortality and the increased importance of competition in the tropics. It is also argued that the latitudinal difference in mortality results in greater restriction to food types and more specific

habitat requirements in the tropics, which in turn allow more species to coexist in a given environment; competition for resources is thus keener, and "niches" smaller, in the more diverse communities.

Thus, the competition hypothesis makes many of the same predictions as the theory of climatic stability, and the two mechanisms could work in series to determine diversity. However, there is one difference between the two hypotheses: the competition hypothesis implies that more individuals occupy the unit of habitat space (or else competition would not be intensified) in more diverse communities, whereas the theory of climatic stability predicts that the same number of individuals will be supported by a unit of habitat, regardless of the diversity (but because each of the component species may be rarer without becoming extinct, there can be more species).

Abundance data from the tropics and temperate zones generally show similar numbers of individual birds per unit area (a crude measure of the "unit of habitat space" in areas of similar spatial complexity and productivity), and therefore support the theory of climatic stability (Klopfer and MacArthur 1960, Skutch 1954, 1960). Flatland desert lizards show no latitudinal trend in the number of individuals per hectare, although there is a crude correlation between overall abundance of all lizard species combined and the recent average annual precipitation (Pianka 1965).

Competition is notoriously difficult to demonstrate among animals in nature (Andewartha and Birch 1954, Kohn 1959), and the present data constitute no exception; however, assessing the degree of competition between these lizards may be attempted by somewhat qualitative and circuitous means. The pronounced differences in microhabitat and methods of foraging between lizard species (Pianka in press) can be supposed to be adaptations which reduce competition; and the very existence of these differences mean that the overlap in diets cannot be used to estimate the intensity of competition.

There is probably little direct competition between such specialized species as *Dipsosaurus, Uma, Coleonyx, Xantusia,* and *Heloderma.* Likewise, it would seem that the arboreal habits of *Urosaurus* and *Sceloporus* should prevent or reduce competition with other lizards, and the division of the tree, as well as the differences in diet and foraging habits suggest that competition between these two species would in turn be very slight. *Coleonyx* probably has no direct lizard competitors due to its strictly nocturnal habits. The other five species (*Cnemidophorus, Uta, Crotaphytus, Phrynosoma,* and *Callisaurus*) exploit the environmental

mosaic in a rather consistent way from north to south, and in view of the lack of a latitudinal trend in their abundances, it seems unlikely that there is any consistent latitudinal change in the amount of competition occurring between these species.

A crude quantitative estimate of the intensity of competition may be constructed as follows. The total amount of food available in the communities should be proportional to the recent precipitation (because precipitation is correlated with primary production), and the demands on this food supply by lizards should be proportional to the overall abundance of lizards (all species combined). Demand divided by availability is thus an index, although admittedly a crude one, of the sum of both the intraspecific and interspecific competition for food. Table 4 gives such ratios for lizards, snakes, insectivorous birds, predaceous birds, and small mammals for each of the study areas. There are clear latitudinal increases in the amount of competition for food in the snakes and predatory birds, with a much lesser trend in the insectivorous birds. Small mammals and lizards display no latitudinal trends in the intensity of competition for food. Because abundances are measured in different units, cross comparisons between the various taxa are difficult. Since both insectivorous and predatory birds are more common per unit of precipitation in the southern deserts than in the north, there is probably increased competition between and among bird species. Although somewhat inconclusive because of differences in energy requirements, these data may also indicate increased competition between lizards and birds in southern deserts (to the extent that their diets overlap).

PREDATION

Following a line of reasoning roughly the converse of the competition hypothesis, the proponents of the predation hypothesis assert that there are proportionately more predators (individuals and/or species) in the tropics, and that, by limiting various prey populations at low densities, the predators reduce the level of competition between and among prey species (Fryer 1965, Paine 1966). It is argued that this lowered level of competition then allows the addition and coexistence of new intermediate prey types (either by migration or speciation), which new prey types would, in turn, support new predator species. Thus, in theory, predation-induced diversity increases continuously and infinitely, and something else must be invoked to set an upper limit on the process. [A variety of suggestions have been made, including the merging of the predation hypothesis with the

TABLE 4. Abundance data and ratios of abundances to recent precipitation. Note that cross-taxa comparisons are useless because abundances are measured in different units and no allowance has been made for differences in metabolic rates (see text)

Taxon	Units	C	W	T	M	S	P	V	G	L	I	U
Lizards	(no./hectare)	11.8	5.5	3.9	9.0	7.5	2.2	3.8	6.8	9.0	5.0	5.2
Snakes	(no./mile)	.104	.101	.083	.081	.090	.057	.083	.020	.053	.028	
Pred. Birds	(no./mile)	.157	.158	.193	.158	.114	.036	.000	.000	.070	.000	
Ins. Birds	(no./mile)	.235	.358	.269	.382	.273	.097	.263	.140	.281		
Sm. Mammals	(no./trap night)	.098	.088	.017	.078	.054	.040	.076	.104	.369	.017	
Average Annual Precipitation during 5 years prior to study (in centimeters)		19.38	12.87	9.75	10.9	14.1	8.66	9.91	9.2	14.8	20.2	17.5
Ratios of abundance to precipitation (decimal points omitted):												
Lizards		608	427	399	825	534	259	387	741	611	252	299
Snakes		536	787	850	743	638	657	837	218	358	128	
Pred. Birds		812	1331	1987	1445	811	416	00	00	474	00	
Insectivorous Birds		121	278	277	350	194	112	266	152	190	?	
Small Mammals		504	682	175	714	383	462	767	1135	264	78	
Percent of the maximum ratio observed for the particular taxon:												
Lizards		.74	.52	.48	1.00	.65	.31	.47	.90	.74	.31	.35
Snakes		.63	.92	1.00	.88	.75	.77	.98	.26	.42	.15	
Pred. Birds		.41	.62	1.00	.73	.41	.21	.00	.00	.24	.00	
Insect Birds		.35	.80	.79	1.00	.55	.32	.76	.43	.54		
Small Mammals		.46	.60	.15	.63	.34	.41	.67	1.00	.23	.07	

productivity hypothesis (Paine 1966), or with the two time theories (Fryer 1965, Greenwood 1965).]

Two predictions may be drawn from the predation hypothesis: (1) competition amongst prey organisms will be less in more diverse communities than it will be in simpler communities, and (2) there should be an increase in the proportion of predatory individuals and/or species as communities become more diverse. There is no available data relating to the first prediction (reduced competition at the lower trophic levels in more complex communities), but several workers have presented evidence that the proportion of predatory species increases in more diverse communities (Grice and Hart 1962, Fryer 1959, Paine 1966).

In lizard populations, the amount of predation may be estimated by the proportion of specimens with tails which have been broken and regenerated. J. B. S. Haldane realized the potential of broken tail frequencies as an estimate of the amount of predation in 1927 (Haldane and Huxley 1927), but only one worker has thus far used them to estimate predation (Rand 1954). In some lizard species, such as *Agama agama* (Harris 1964) and *Dipsosaurus dorsalis* (Norris 1953), males break each other's tails during territorial displays and other aggressive encounters, resulting in significantly higher percentages of broken tails than in females. Female lizards may also occasionally break one another's tails, but no sys-

tematic data are presently available. Other differences in the behavior of the two sexes might also result in different susceptibilities to predation, and the interpretation of broken tail data is therefore difficult. In order to determine whether or not they are independent of intra-specific fighting, all broken tail percentages were first plotted against the species density divided by the recent precipitation (this procedure was necessary because fighting should be directly proportional to lizard density and inversely proportional to the availability of food, which itself is directly dependent on the recent precipitation). Males and females were analyzed separately, but usually showed similar trends. Significantly higher proportions of broken tails were found in southern populations than occurred in the north in four of the five wide ranging species (*Cnemidophorus, Uta, Phrynosoma,* and female *Callisaurus*), while the fifth species (*Crotaphytus*) showed the same trend but the sample was too small for significance.

Data on snake predators shows a slight increase in the abundance of lizard-eating snakes per unit area of desert at lower latitudes, but a tripling of the number of snake species. Avian predators include various buteos, roadrunners, prairie falcons, burrowing owls, kestrels, shrikes, thrashers, ravens and crows. The four northern most study sites lacked avian predators, while the six southern ones had from .036 to .193 lizard-eating birds per mile. It is therefore fairly likely that there

are proportionately more lizard predators per unit area of desert in the south than there are in the north. The number of bird species known to eat lizards increased from zero on the northern three sites to six species on the southernmost area. This is partially due to the generally greater diversity in southern deserts, one of the concomitant and natural consequences of greater community complexity being more species of predators. However, it is clear from the foregoing evidence that there is proportionately greater predation upon the southern lizards than there is upon the northern ones. The predation hypothesis does not lend itself to the suggestion of direct causal mechanisms concerning individual species, and it is therefore difficult to assess the importance of predation as a factor controlling the number of lizard species.

Discussion and Conclusions

Only two of the correlations with the number of lizard species appear to be potentially causal (those with growing season and spatial heterogeneity) and require distinguishing. Multiple regression could not be used to separate the relative importance of growing season and spatial heterogeneity because these two independent variables are strongly interrelated. It is likely that this interrelation has a causal basis of its own, as described earlier, in that climate probably controls vegetative structure which in turn controls lizard diversity.

Thus, the number of species of flatland desert lizards occurring together may be explained with recourse to only three of the eight mechanisms which have been proposed: the ecological time theory (*Uma*), the stability of primary production hypothesis (*Coleonyx, Heloderma,* and perhaps *Dipsosaurus*), and, in its broadest sense, the theory of spatial heterogeneity (the 8 remaining species and perhaps *Dipsosaurus*). The predation hypothesis may also be important, but need not be invoked to explain the gradient. For the most part, climate exerts its effect on the lizard diversity gradient indirectly, by way of its direct influence upon the vegetation and soils. Shreve (1942) has suggested that climatic variability creates physical spatial heterogeneity by erosion, and that the multitude of plant life forms found in desert regions are a result of the variability of rainfall. The relatively stable pattern of rainfall in the Great Basin desert exerts a restricting influence on the number of plant life forms (and therefore upon the number of lizard species) supported by that desert.

It is premature to extrapolate from these tentative conclusions on the flatland desert-lizard system to the problem of temperate vs. tropical diversity, but it is hoped that this and other studies along diversity gradients will help pave the way towards a general theory. Only after a fair number of different taxa have been studied will we be able to perceive the underlying and unifying features of the partitioning of biotope space by various plant and animal groups in different physical and biotic environments.

Literature Cited

Andewartha, H., and L. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago, Ill.

Anonymous. 1941. Climate and Man. U.S. Dept. Agr. year-book, 1941.

Axelrod, D. I. 1949. Discussion in "Sedimentary facies in Geologic History." Mem. Geol. Soc. Amer. No. **39**: 155–164.

———. 1950. The evolution of desert vegetation. Carnegie Inst. of Washington, pub. No. **590**: 216–306.

———. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. **24**: 433–509.

Banta, B. H. 1961. The variation and zoogeography of the lizards of the Great Basin. Ph.D. Thesis, Stanford Univ. Diss. Abstr. **22**: 1361.

———. 1962. Preliminary remarks upon the zoogeography of the lizards inhabiting the Great Basin of the western United States. Wasmann J. Biol. **20**: 253–287.

Blaisdell, J. P. 1958. Seasonal development and yield of native plants on the upper Snake River plains and their relation to certain climatic factors. U.S. Dept. Agr., Tech. Bull. No. 1190.

Broecker, W., and P. Orr. 1958. The radio-carbon chronology of Lake Lahontan and Lake Bonneville. Bull. Geol. Soc. Amer. **69**: 1009–1032.

Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. Amer. Naturalist **98**: 399–414.

Crowell, K. 1961. The effects of reduced interspecific competition in birds. Proc. Nat. Acad. Sci. **47**: 240–243.

————. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology **43**: 75-88.

Deevey, E. S., Jr. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Amer. **60**: 1315–1416.

Dobzhansky, T. 1950. Evolution in the tropics. Amer. Scientist **38**: 209–221.

Elias, M. K. 1942. Tertiary prairie grasses and other herbs from the high plains. Geol. Soc. Amer., special papers, no. 41.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, England.

Fautin, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr. **16**: 251–310.

Finch, V. C., and G. T. Trewartha. 1949. Physical elements of geography. McGraw-Hill Book Company, Inc., New York, Toronto, London. (p. 151).

Fischer, A. G. 1960. Latitudinal variation in organic diversity. Evolution **14**: 64–81.

Fisher, R. A. 1958. Statistical methods for research workers. Hafner Publishing Company, Inc., New York, N.Y.

Fisher, R. A., and F. Yates. 1963. Statistical tables for biological, agricultural, and medical research. Oliver and Boyd, London, England.

Fryer, G. 1959. Some aspects of evolution in Lake Nyasa. Evolution **13**: 440–451.

————. 1965. Predation and its effects on migration and speciation in African fishes: a comment. Proc. Zool. Soc. London **144**: 301–322.

Garman, E. H. 1955. Regeneration problems and their silvicultural significance in the coastal forests of British Columbia. B. C. Forest Service, Tech. Pub. No. **T. 41**: 67 pp.

Gilmore, C. W. 1928. Fossil lizards of North America. Mem. Nat. Acad. Sci. **22**: 1–201.

Greenwood, P. H. 1965. A further comment. Proc. Zool. Soc. London **144**: 310–313.

Grice, G. D., and A. D. Hart. 1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. **32**: 287–309.

Hairston, N. G. 1959. Species abundance and community organization. Ecology **40**: 404–416.

Haldane, J. B. S., and J. Huxley. 1927. Animal biology. Oxford Univ. Press, London (pp. 175–176).

Harris, V. A. 1964. The life of the rainbow lizard. Hutchinson Trop. Monogr., Hutchinson & Co. (Publishers) Ltd., London.

Keen, F. P. 1958. Cone and seed insects of western forest trees. U.S. Dep. Agr., Tech. Bull. No. 1169 (168 pp.).

Klopfer, P. H. 1959. Environmental determinants of faunal diversity. Amer. Naturalist **93**: 337–342.

Klopfer, P. H., and R. H. MacArthur. 1960. Niche size and faunal diversity. Amer. Naturalist **94**: 293–300.

————. 1961. On the causes of tropical species diversity: niche overlap. Amer. Naturalist **95**: 223–226.

Kohn, A. J. 1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. **29**: 47–90.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. Amer. Naturalist **98**: 387–398.

————. 1965. Patterns of species diversity. Biol. Rev. **40**: 510–533.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology **42**: 594–598.

MacArthur, R. H., J. W. MacArthur and J. Preer.

1962. On bird species diversity: II. Prediction of bird census from habitat measurements. Amer. Naturalist **96**: 167–174.

MacArthur, R. H., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Amer. Naturalist **100**: 319–332.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution **17**: 373–387.

MacPherson, A. H. 1965. The origin of diversity in mammals of the Canadian Arctic tundra. Syst. Zool. **14**: 153–173.

Margalef, D. R. 1957. Information theory in ecology. (reprinted in 1958). Gen. Syst. **3**: 37–71.

Martin, P. S., and P. J. Mehringer, Jr. 1965. Pleistocene pollen analysis and biogeography of the southwest. in: The Quaternary of the U.S., a review volume for the VII Congr. Int. Ass. Quaternary Res., Wright and Fry, editors. Princeton Univ. Press, Princeton, N.J.

Merriam, J. and W. Sinclair. 1907. Tertiary faunas of the John Day region. Publications of the University of California, Bull. Dep. Geol. Sci. **5**: (11): 171–205.

Miller, A. H. 1958. Ecologic factors that accelerate formation of races and species in terrestrial vertebrates. Evolution **10**: 262–277.

Mosauer, W. 1932. Adaptive convergence in the sand reptiles of the Sahara and of California. Copeia **1932**: 72–78.

Newell, N. D. 1962. Paleontological gaps and geochronology. J. Paleontol. **36**: 592–610.

Norris, K. S. 1953. The ecology of the desert iguana, *Dipsosaurus dorsalis*. Ecology **34**: 265–326.

————. 1958. The evolution and systematics of the iguanid genus *Uma* and its relation to the evolution of other North American desert reptiles. Bull. Amer. Mus. Natur. Hist. **114**: 247–326.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Naturalist **100**: 65–75.

Pearson, L. C. 1965. Primary production in grazed and ungrazed desert communities of eastern Idaho. Ecology **45**: 278–286.

Pianka, E. R. 1965. Species diversity and ecology of flatland desert lizards in western North America. Ph.D. Thesis, Univ. of Washington, Seattle, Wash. Diss. Abstr. **27**: 334-335B.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Amer. Naturalist **100**: 33–46.

Rand, A. S. 1954. Variation and predator pressure in an island and a mainland population. Copeia **1954**: 260–262.

Ricklefs, R. E. 1966. The temporal component of diversity among species of birds. Evolution **20**: 235–242.

Shannon, C. E. 1948. The mathematical theory of communication. In Shannon and Weaver, The mathematical theory of communication. Univ. of Illinois Press, Urbana, Ill.

Shreve, F. 1942. The desert vegetation of North America. Bot. Rev. **8**: 195–244.

————. 1951. Vegetation of the Sonoran desert. Carnegie Inst. of Wash., Pub. No. 591. (reprinted 1964 by Stanford Univ. Press, Stanford, Calif.)

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, Inc., New York, Toronto, London.

Simpson, G. G. 1964. Species density of North American recent mammals. Syst. Zool. **13**: 57–73.

Skutch, A. F. 1954. Life histories of central American birds. Vol. I. Cooper Ornithol. Soc., Pacific Coast Avifauna No. **31**.

————. 1960. Life histories of central American birds. Vol. II. Cooper Ornithol. Soc., Pacific Coast Avifauna No. **34**.

Smith, C. C. 1965. Interspecific competition in the genus of tree squirrels *Tamiasciurus*. Ph.D. Thesis, Univ. of Washington, Seattle, Wash. (268 pp.) Diss. Abstr. **26**: 4909.

Snedecor, G. W. 1956. Statistical methods applied to experiments in Agriculture and biology. Iowa State Univ. Press. Ames, Iowa.

Stebbins, G. L., Jr. 1947. Evidence on rates of evolution from the distribution of existing and fossil plant species. Ecol. Monogr. **17**: 147–158.

Stebbins, R. C. 1954. Amphibians and reptiles of western North America. McGraw-Hill Book Company, Inc., New York, Toronto, London.

Terent'ev, P. V. 1963. Opyt primeneniya analiza variansy k kachestvennomu bogatstvu fauny nazemnykh pozvonochnyk. (Attempt at application of analysis of variation to the qualitative richness of the fauna of terrestrial vertebrates of the U.S.S.R.). Vestnik Leningradskovo Univ. **18** (21: 4): 19–26. (English abstract in Biol. Abstr. **45**: 80822.)

U.S. Weather Bureau. 1930. Bull. "W" (reprinted in 1952).

U.S. Weather Bureau. 1952. Suppl. to Bull. "W," 1931–1951.

U.S. Weather Bureau. 1953–1965. Climatological data. (series by states).

Visher, S. S. 1954. Climatic atlas of the United States. Harvard University Press, Cambridge, Massachusetts (403 pp.).

Walter, H. 1939. Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. Jahrbucher für wissenschaftliche Botanik **87**: 750–860.

————. 1955. Le facteur eau dans les regions arides et sa signification pour l'organisation de la vegetation dans les contrees sub-tropicales. In: Colloques Int. du Centre National de la Recherche Sci. Vol. **59**: Div. Ecol. du Monde. pp. 27–39. Centre Nat. de la Recherche Sci., Paris (236 pp.).

————. 1964. Productivity of vegetation in arid countries, the savanna problem, and bush encroachment after overgrazing. Proceedings and Papers of the I.U.C.N. 9th Technical Meeting (Nairobi, September 1963); I.U.C.N. Publications new series No. 4 (1964). Part III. "The Impact of Man on the Tropical Environment," pp. 221–229.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, New York and London (p. 4).

RADIOISOTOPE TURNOVER AND ENERGY FLOW IN TERRESTRIAL ISOPOD POPULATIONS[1]

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Abstract. Radiocesium turnover rates in terrestrial isopod populations were used to measure food consumption and metabolism under natural and laboratory-simulated field conditions. Four old-field and forest species were studied: *Armadillidium vulgare* (Latreille), *Armadillidium nasatum* Budde-Lund, *Cylisticus convexus* (DeGeer), and *Metoponorthus pruinosus* (Brandt). Uptake, body burden equilibria, and elimination rates for ^{134}Cs were related to environmental temperatures ($Q_{10} \simeq 2$). Dietary supplements of stable Na, K, and Cs salts produced no effect upon ^{134}Cs elimination rates. Assimilation fractions from food were 60 to 64% for digestible dry matter, 70 to 73% for caloric intake, and 70 to 87% for radiocesium. Body equilibrium concentrations and biological half-lives of radiocesium in each species permitted estimates of food consumption comparable to gravimetric determinations. Food intake varied between different species and ranged from 1.5 to 3.5% of dry body weight per day. Bomb calorimetry and respirometry measurements were used to partition the total energy budgets, caloric inputs required for maintenance, production, and growth were determined. Radiocesium elimination rates were correlated with the metabolic rates of individual species, and radionuclide turnover rates in tagged individuals were demonstrated to be a practicable means of determining the activity and metabolism of species in their natural habitats.

INTRODUCTION

Radiotracer techniques have been used in various phases of biological research to study the nature and rates of physiological processes. Recently this methodology has been employed in ecological problems dealing with food chain kinetics and trophic relationships in natural ecosystems. By examining uptake rates of ^{32}P, Ball and Hooper (1963) demonstrated that quantitative distinctions could be made between the trophic levels of a stream ecosystem. Paris and