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POPULATION STRUCTURE AND SURVIVORSHIP IN SOME COSTA RICAN LIZARDS

By

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Interest in tropical communities and insight into their functioning have developed at an accelerating pace in recent years. Lizards often are present in great variety and in high population numbers; thus they can be sampled readily, and provide excellent material for demographic studies potentially significant to a knowledge of community ecology. However, there have been few studies of tropical lizard populations, especially in the Neotropical Region. The present study of tropical lizard populations was undertaken in 1965. By obtaining information on the life histories and demography of a substantial number of diverse species of tropical lizards within a limited geographic area, I was able to compare these data with similar data available for the Temperate Zone. Because several of the species included have close relatives in temperate climates, it was anticipated that comparative study of life history and demography would elucidate evolutionary trends in tropical and temperate environments.

A number of studies has been made of the reproduction and population biology of Old World tropical lizards (mainly agamids, geckos and skinks). Among these are studies in central and west Africa (Marshall and Hook, 1960; Harris, 1964), India (Asana, 1931; Pandha and Thapliyal, 1967; Sanyal and Prasad, 1967), Borneo (Inger and Greenberg, 1966), the Philippines (Alcala and Brown, 1967), the New Hebrides (Baker, 1947) and Australia (Wilhoft, 1963; Wilhoft and Reiter, 1965; Bustard, 1968, 1969; Pianka, 1971). There have been few comparable studies of Neotropical lizards. Those of Hirth (1963) on *Ameiva quadrilineata*

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and *Basiliscus vittatus* and Sexton *et al.* (1963, 1971) on *Anolis limifrons* are notable.

Some outstanding population studies of lizards in the United States are those of Blair (1960) on *Sceloporus olivaceus*, Tinkle (1967) on *Uta stansburiana* and Kennedy (in press) on *Sceloporus undulatus*. Many other studies, though less intensive or prolonged, have revealed some population parameters of the species investigated. For example, it has been shown that most lizards in the southern half of the United States mature in their first year after one season of hibernation, and most produce two or more broods in each breeding season. Included in the latter group are: *Sceloporus undulatus; S. olivaceus; S. jarrovi* (Carpenter, 1960); *Uma inornata, U. notata, U. scoparia* (Mayhew, 1964a, 1964b, 1966a, 1966b); *Uta stansburiana; Crotaphytus collaris* (Fitch, 1956); *Crotaphytus wislizenii* (Turner, *et al.*, 1969); *Leiolopisma laterale* (Fitch and Greene, 1965) and *Cnemidophorus sexlineatus* (Fitch, 1958). Among species that range farther north, such as *Sceloporus occidentalis, S. graciosus,* and *Eumeces fasciatus,* maturity is delayed until the second year and one brood per season is the rule (Fitch, 1954, 1970). In a few, such as *Eumeces obsoletus* (Hall, 1971), *Ophisaurus attenuatus* (Fitch, 1970), and *Xantusia vigilis* (Miller, 1951), maturity is postponed until the third or even the fourth year and only one brood is produced per season. Consequently, one can conclude that the foregoing species and temperate zone species in general, are characterized by populations consisting of discrete annual age groups. Most lizards in temperate regions hibernate, and some spend as much as two-thirds of the year in continuous dormancy. In general, the longer the hibernation the more pronounced is the seasonal restriction of the breeding cycle; thus such events as ovulation, spermatogenesis, and copulation occur only at certain times of year, and breeding occurs in the early part of the season of activity. In the warmer parts of the temperate region, lizards such as *Uta stansburiana* and various kinds of *Sceloporus* are active intermittently even in winter; they either do not hibernate at all, or have only brief periods of incomplete dormancy. In these species, as well as those that have more complete hibernation, reproduction is controlled by the seasonality of the annual cycle. Reproduction occurs in spring and early summer, and rarely extends into late summer or autumn. The following study of Costa Rican lizards was undertaken in order to describe population parameters of tropical species and thereby facilitate comparison of these with their near relatives in the Temperate Zone. Also, I have attempted to assess the effects of relatively uniform year-round climates as contrasted with climates that are strongly seasonal.

In recent literature pertaining to tropical ecology, various predictions, rules, and models have been proposed; some are based on actual data and others on purely theoretical considerations. Both types require supporting evidence from further field studies. An attempt is made below to examine critically such proposals, including those pertaining to lizards (Tinkle, Wilbur and Tilley, 1970) and those of a more general sort—*r*-selection and *K*-selection (MacArthur and Wilson, 1967; Pianka, 1970), and "coarse-grained" vs. "fine-grained" environments—in the light of my own findings.

Methods and Materials

In February and March 1965 I collected samples of lizards at several localities in Costa Rica. In October and November 1967 I selected 14 localities for study areas in Costa Rica; several of these had been sampled in 1965, and form transects across the country from east to west and from north to south representing the main climatic types. On these areas, populations of lizards were sampled at intervals averaging approximately six weeks, from October 1967 to September 1968, with further sampling in January-March 1969, August-September 1969 and January-March 1970.

From west to east (localities 1-11) and north to south (localities 6 and 12-14) locations of the study areas, and their most important species of lizards are as follows: 1) Playas del Coco, Guanacaste Province, sea beach and thorny scrub, with open groves and a few large trees: *Sceloporus variabilis* Wiegmann, *Cnemidophorus deppii* Wiegmann, *Ctenosaura similis* (Gray). 2) Sardinal, Guanacaste Province, 90 m, gallery forest along ravine: *Anolis cupreus* Hallowell. 3) Río Higuerón at Finca Taboga, Guanacaste Province, lowland xeric riparian forest and grassland: *Basiliscus basiliscus* (Linnaeus) and *Ctenosaura similis.* 4) Río Congo at La Irma, Guanacaste Province, 100 m, riparian groves and dry pastures: *Anolis cupreus* and *Basiliscus basiliscus.* 5) Boca de Barranca, Puntarenas Province, sea beach and Marbella Hotel grounds, with many native and exotic trees: *Sceloporus variabilis, Cnemidophorus deppii, Gonatodes albogularis* (Duméril and Bibron), *Anolis cupreus* and *Ctenosaura similis.* 6) San José, San José Province, 1197 m, suburban lots with scattered trees and tall grass; fences along railway and coffee groves: *Anolis cupreus, Anolis intermedius* Peters, and *Sceloporus malachiticus* Cope. 7) Cartago, Cartago Province, 1450 to 1750 m, roadside rock outcrops; rocky and brushy pasture: *Sceloporus malachiticus.* 8) Turrialba, Instituto Interamericano de Ciéncias Agrícolas, Cartago Province, 602 m, groves and plantations: *Anolis limifrons* Cope and *Leiolopisma cherriei* (Cope). 9) Portéte, Limón Province, sea beach with coral rock and coconut grove: *Basiliscus vittatus* Wiegmann. 10) Limón, Limón Province, seaside city park with giant fig trees: *Gonatodes albogularis.* 11) Beverly, Limón Province, 15 m, banana and cacao groves: *Anolis limifrons* and *Anolis humilis* Peters. 12) San Miguel de Sarapiquí, about 500 m, Alajuela Province, subtropical rain forest along mountain stream: *Anolis humilis* and *Anolis lionotus* Cope. 13) Hacienda El Prado, 1910 m, Alajuela Province, pasture with relict trees of original cloud forest: *Anolis tropidolepis* Boulenger. 14) Quepos, Puntarenas Province, sea beach at mouth of Río Cañas, with open sand, beach wrack deposited by the river, coconut grove, and mangrove swamp: *Ameiva quadrilineata* (Hallowell) and *Ctenosaura similis.*

Most lizards captured were measured and marked with paint, and toe-clipped to facilitate individual recognition. Relatively few of the individuals recorded in a sample are represented in the next sample from the same area because population turnover due to mortality, natality, emigration and immigration is relatively rapid on all areas. Even under optimum conditions it was never possible to record all individuals present on any specific area. Findings regarding growth, temperature relationships, spatial relationships and reproductive cycles have been discussed elsewhere (Fitch, 1973).

Various methods, including trapping, noosing, and catching by hand, were utilized in obtaining lizards. However, some abundant species are too wary and elusive to be captured by any of the usual methods. In these species snout-vent length was estimated to the nearest mm in individuals seen at close range in the field. On many occasions the same lizard was first estimated and then captured and measured; these sets of records provided a basis for judging the accuracy of the estimates. Estimates were usually within 2 percent.

Some samples (*Anolis tropidolepis, A. humilis, A. limifrons, Sceloporus variabilis, Leiolopisma cherriei, Gonatodes albogularis* at Boca de Barranca) are based entirely upon actual measurements of individuals captured and handled. Other samples (*Gonatodes albogularis* at Limón, *Ameiva quadrilineata*) are based mainly on estimates, and some (*Cnemidophorus deppii, Basiliscus basiliscus, B. vittatus, Ctenosaura similis*) are based upon both sorts of data.

Histograms (Figs. 1-17) show composition by size groups of the populations sampled. Seasonal trends are strong in some and weak in others. In some instances (*Sceloporus variabilis, Anolis tropidolepis, A. intermedius*), sex could be determined readily even in hatchlings; thus sex ratio is shown for each size category in the population. In most kinds, sex is less readily discerned in the young and is shown only for the sexually mature size classes. In *Ctenosaura similis, Cnemidophorus deppii* and *Ameiva quadrilineata* sex often was not determined in the observed adults. In both species of *Basiliscus,* adult males are readily distinguished from females, but adolescent males and adult females are much alike in size and appearance; therefore sexes are not shown separately on the graph.

In the histograms, samples from February and March are composites from 1968, 1969 and 1970. Likewise, samples from August and September of 1968 and 1969 were combined. Samples from April, May, June, and July are exclusively from 1968 and samples from October and November are from 1967. In the upper left of each figure, three horizontal bars show the size range considered typical for young in their first, second and third months, respectively. These are based on the average growth rates of recaptured marked young of different sizes, but with some subjective judgments to allow for the slight stunting that occurs at first after toe-clipping, and the difficulty of distinguishing newly hatched indiviuals from those that have already made some growth. Dotted extensions of each bar represent estimates of the size range for the majority of individuals including those that exceed the most typical growth rate or fall short of it.

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RESULTS

In the present study, populations are partially analyzed by segregation into sex- and size-groups. On the basis of growth of numerous young marked and recaptured, size can be equated with age to some extent, especially in the immature lizards. Judged on the basis of its size and appearance, each individual has a fairly wide range of possible ages, but has one "most probable" age that can be calculated from the average growth rate at each stage of development.

Population structure rarely has been mentioned in published reports upon field studies of lizards. Often there are differences in behavior (that may cause differences in susceptibility to capture) between the sexes and between young and adults, so that any sample obtained is somewhat biased. Growth rates may vary widely from time to time and place to place, or between individuals, and the status of any individual in the population can be known with certainty only if it was marked as a hatchling. In the tropics there is more complexity and diversity than in the Temperate Zone where most populations of lizards have two or more size classes, sometimes discrete and sometimes widely overlapping. Size classes result from discontinuous reproduction and the fact that each population consists of a series of cohorts, ranging in age from the young (normally the most numerous and most distinct) to the old; the latter are few in number not readily distinguishable from the next younger cohort. The population structure can remain stable only in an unchanging environment where reproduction goes on continuously at a constant level.

In every population sample that I obtained, there is possibility of bias. For example, gravid females of *Cnemidophorus deppii* are noticeably slower and less elusive than adult males, and therefore are better represented in my samples. Similarly, in *Basiliscus basiliscus* old adults are much more wary than juveniles and tend to stay nearer shelter. However, successive samples from the same areas were presumably all subject to the same bias, and therefore should reflect fairly accurately the changes in population structure that occur throughout the year.

Information concerning longevity in free-living lizards is also scarce and difficult to obtain. Mark-and-recapture studies usually have not been pursued with sufficient intensity or continued for a sufficient length of time to demonstrate longevity. The 29-month span of operations on some of my study areas perhaps was inadequate to demonstrate longevity in any of the species studied. but it does permit comparison of the rates of population turnover. The rate of turnover is closely linked with survivorship; species having the longest life expectancy have relatively slow turnover. However, vagility, the degree of unnatural disturbance to which a study area is subjected, and the size of the study area all affect population turnover, and in some instances these effects are independent of mortality. A population consisting partly of transient individuals or one in which frequent changes in home range occur, would show turnover even without any mortality. In all of the species included in my study, recapture records have shown that home ranges are remarkably small, but in each kind there are occasional long movements. On small study areas such movements can affect appreciably the amount of population turnover. The "survivorship" of various species shown in figures 18 and 19 is probably somewhat reduced in each instance by movement away from the study areas, but in most instances disappearance from the study areas is believed to result from actual mortality.

The 21 local populations sampled show a remarkable diversity in their structure and stability; no two of them are alike. In some instances the same species sampled in different areas show notably altered patterns. In other instances a species sampled in areas having somewhat different climates has similar or parallel trends; in some of these (*Anolis humilis*, *Sceloporus malachiticus*) samples from different areas were combined to increase sample size. Different species of lizards sampled at the same times and places often differed strikingly in the structure and stability of their populations. Therefore, generalizations are difficult to make, but there are trends which are correlated with climate, with habits and habitat of the species, and with phylogenetic relationships. The populations sampled could be arranged in various ways to emphasize their similarities or differences. They form a gradient. At one extreme are species that have constant reproduction with females producing offspring frequently and acyclically. At the other extreme are species in which individuals reproduce only once in the annual cycle, and all produce at about the same time, resulting in a population of well defined and separate annual cohorts. For convenience and clarity I prefer to recognize four distinct types of populations, although these grade into each other to some extent. A type 1 population, with stable age structure is relatively uncommon and results from year-round reproduction at a constant level. A type 2 population also has year-round reproduction but with changing level in response to the seasonal weather cycle, resulting in a fluctuating age structure. A type 3 population is characteristic of areas having a severe dry season which inhibits reproduction, resulting in a seasonally changing structure, with mostly adults at some times of year and mostly immatures at other times. A type 4 population results from a short annual breeding season and delayed maturity.

The Type 1 Population.—In the type 1 population there is no temporal change in the level of reproduction and stability has been attained. Individuals of all sizes and ages are constantly present in the population in unvarying ratios. Four of the 21 populations sampled fit best with type 1, but none fits perfectly. The best fit is an anole of montane cloud forest on the continental divide, and the remaining three are species of a warm, wet climate in the Caribbean lowlands. In some instances differences between successive samples may have been due to chance and inadequate sample size, but in most instances the differences probably reflect small changes in the level of reproduction or reproductive success, that are responses to weather and climate.

At Hacienda El Prado the cloud forest habitat of *Anolis tropidolepis* is always cool and moist. Temperature change from winter to summer is only about 3°C (Fitch, 1972). Although precipitation is greatly reduced in February and March, moisture shortage does not become critical. Mist and drizzle are frequent even in the driest part of the year. There is never a scarcity of drinking water nor of moist sites for egg-laying. Cloud cover is variable and often persistent, but because these lizards carry on their activities at relatively low temperatures without basking, they are not handicapped by lack of sunshine.

Analysis of eight samples from different times of year shows that

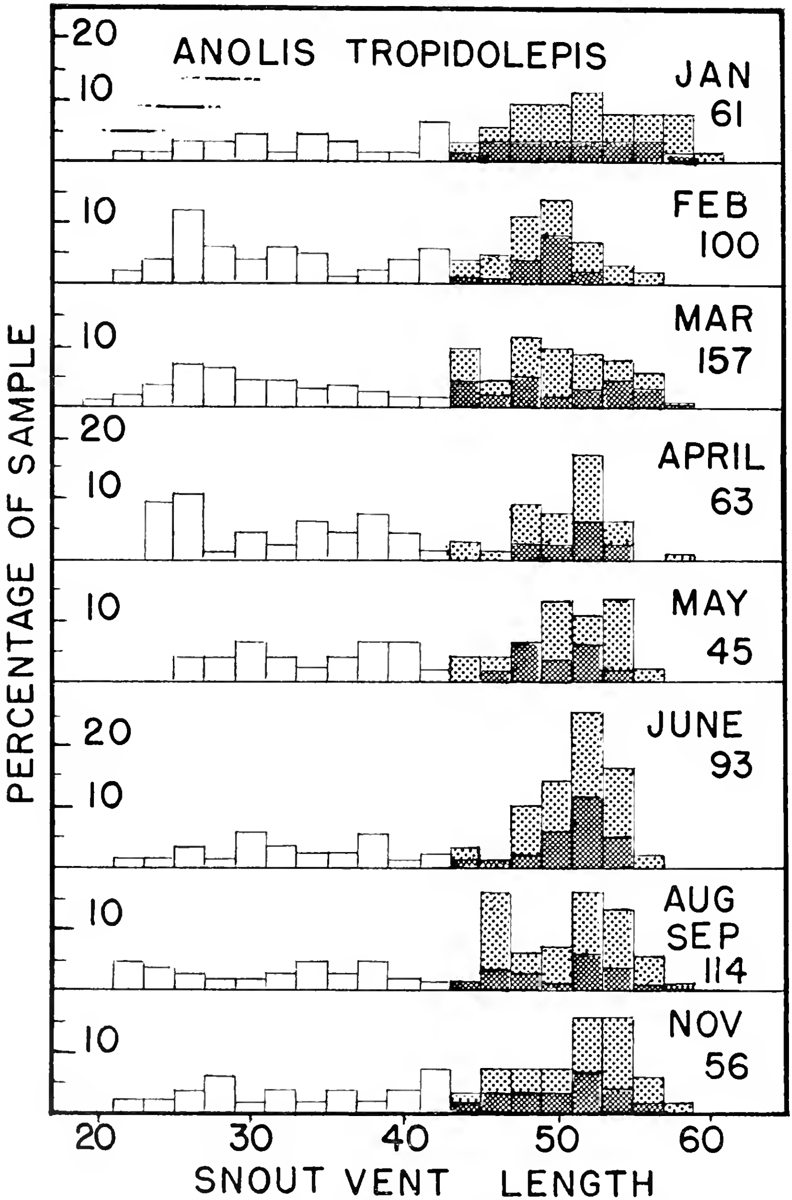

FIG. 1.—Population structure (Type 1) in *Anolis tropidolepis* at Hacienda El Prado. Individuals are grouped into eight seasonal categories and into 2-millimeter size classes for each period. Open columns show immatures, lightly shaded columns are adult males, and heavily shaded columns are adult females. Lines at left show usual size range of first-, second-, and third-month young, and numbers at right show sample sizes.

in each sample the greatest concentration of individuals is in the size range of 49 to 55 mm, small to medium adults. Young (23-29 mm) in their first few weeks of life also are well represented, and throughout the year individuals of every size (and age) from hatchlings (23 mm) up to large adults (57 mm) are present (Fig. 1). Every adult female examined was gravid. There is continuous production of eggs throughout the year, with an average interval of about 30 days between ovipositions for a given female.

Anolis humilis also represents a type 1 pattern (Fig. 2). Its habitat is in leaf litter and on buttressed roots in rain forest. Seasonal change in its habitat is slight. October, November, and December are missing from the samples. The data are from pooled samples from Beverly and San Miguel de Sarapiquí, because there are no obvious differences in the trends between these localities, which are 132 km apart and represented by comparable numbers of records. On the average, the females of *Anolis humilis* are larger than the males. All adult females in each of the eight months of sampling appeared to be gravid; presence of eggs (one uterine egg

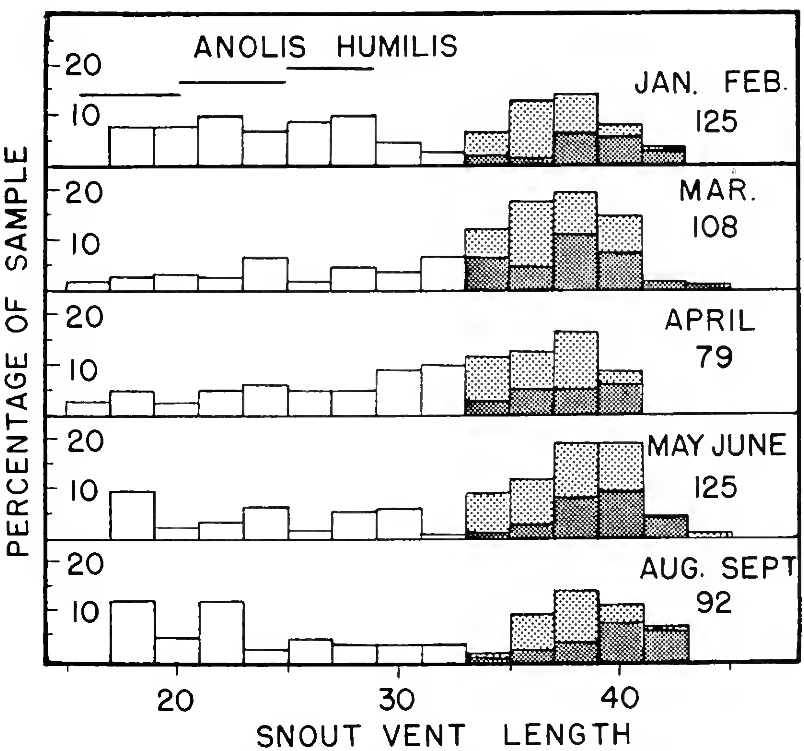

FIG. 2.—Population structure (Type 1) of *Anolis humilis* as shown by combined samples from Beverly and San Miguel de Sarapiquí. Explanation as in Fig. 1.

on each side, or on one side with an enlarged ovarian follicle on the other) was confirmed in the 78 that were actually dissected. Small young are least well represented in March, April, May, and June; this suggests some reduction of the rate of reproduction in the drier part of the year, but there is no true dry season within the range of *A. humilis*.

Also present on the study area at San Miguel de Sarapiquí is *Anolis lionotus*, a semi-aquatic species usually found on bare rocks or cobble at the edge of swift mountain streams. *Anolis lionotus* seems to conform with the type 1 pattern but only 42 are recorded on my study area, and some parts of the year are not represented. The best sample consists of 20 anoles obtained on 16 and 17 April; there are graduated sizes from hatchlings to large adults. All adult females examined appeared to be gravid, and 17 in the University of Kansas Museum of Natural History, from various localities in Costa Rica in January, June, July, and August contain eggs.

Gonatodes albogularis from the city park in Limón in the Caribbean lowlands also seems to conform to a type 1 pattern (Fig. 3). Each sample contains young of various age groups and adults, with no well defined seasonal change discernible among the samples. The high population density, low ratio of hatchlings and other young to adults, and relatively small average and maximum size in adults of this urban population are thought to be symptoms of overcrowding and cannibalism in the absence of the usual predators. Samples from the Pacific Coast at Boca de Barranca, in a seasonably dry climate (Fig. 16) are much different, showing a type 3 pattern, with a high ratio of young for most of the year.

The Type 2 Population.—In type 2 populations, reproduction is continuous throughout the year, but its level changes in response to climatic factors in areas where there is some seasonality. As a result, individuals of all ages are always present but in constantly changing ratios. Presumably the sequence of change is repeated regularly in each annual cycle. The amount of change differs greatly among populations of different species and covers a wide range between type 1 and type 3. Type 2 is the prevalent pattern for most species in the Caribbean lowlands. In this region, which originally was mostly rain forest, the climate is warm and generally wet, but with relatively dry weather in February, March, and April. Possibly in dry periods reproduction is inhibited by limited supplies of drinking water and of sites for egg-laying. Probably more important are the reduced supplies of insect food during dry periods.

Ameiva quadrilineata sampled at Quepos (Fig. 4) is typical of type 2. Reproduction continues throughout most or all of the year, but there is seasonal change in the level of reproduction resulting in changed composition of the population. Depressed or halted production in the dry season, January to April, results in a scarcity of small young in late spring and early summer, and a

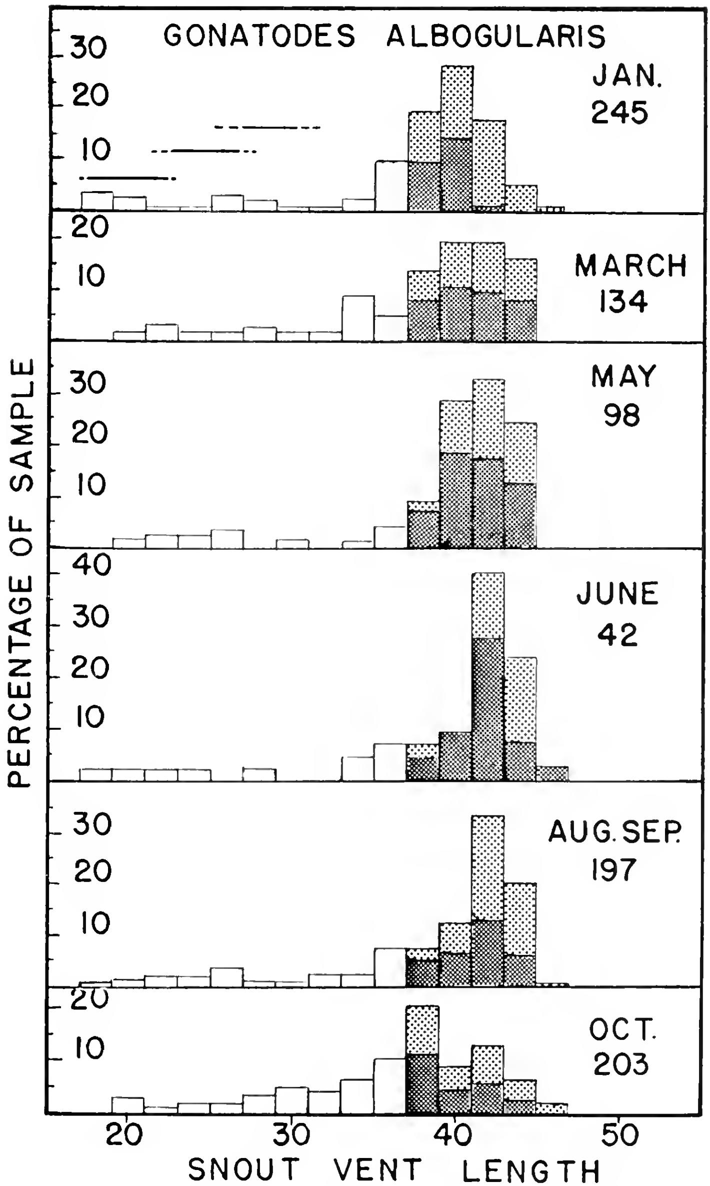

FIG. 3.—Population structure (Type 1) in *Gonatodes albogularis* at Limón. Explanation as in Fig. 1.

scarcity of middle-sized lizards in late summer when a new crop of hatchlings has appeared. Successive increments of young accumulate through the wetter part of the year; growth is remarkably rapid, so that by the dry season the population is rather evenly

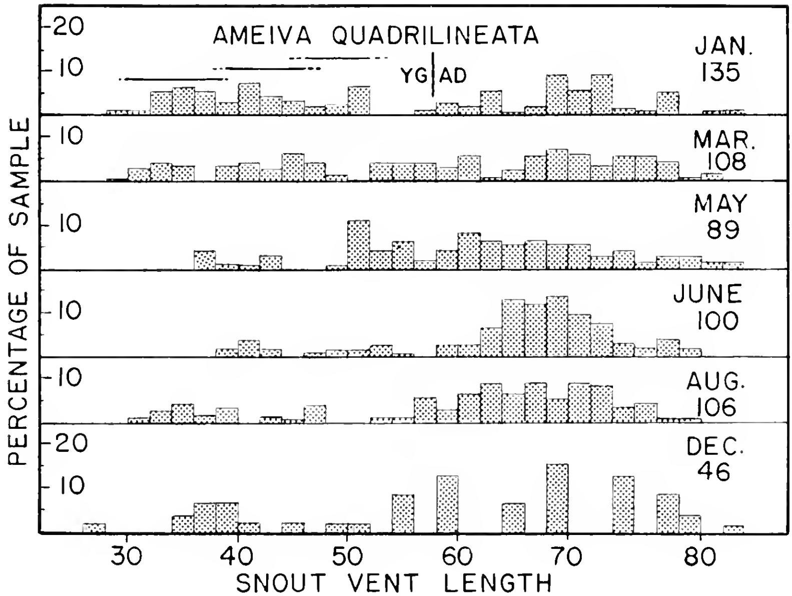

FIG. 4.—Population structure (Type 2) in *Ameiva quadrilineata* at Quepos. Explanation as in Fig. 1, but sex is not shown, and an arbitrary dividing line between (most) young and (most) adults is indicated.

distributed among all size groups. In the Caribbean versant, where the annual precipitation is more evenly distributed, egg production changes less. At Tortuguero, Limón Province, Costa Rica, Hirth (1963) found evidence that the peak of egg-laying is in May and June; thus young are most abundant in August and September, although some hatching continues throughout the year. In the even wetter climate of Pandora in southern Limón Province, Smith (1968) found that all mature females were gravid and concluded that there is uninterrupted reproductive activity throughout the year.

Anolis limifrons was found to be one of the most abundant species, and large, year-round samples were obtained at both Beverly and Turrialba (Figs. 5 and 6). At both localities anoles of all sizes are present throughout the year, but young constitute only a small percentage of the total in April and May (after several months of below-average precipitation) and increase to a majority of the total in October and November late in the rainy reason.

The population structure of *Basiliscus vittatus* at Portéte parallels that of *Anolis limfirons* in its seasonal trends; thus a few small young are present during the driest part of the year (February to April) or immediately after it, but the proportion of young increases in the wetter part of the year (Fig. 7). At Tortuguero, 79 km

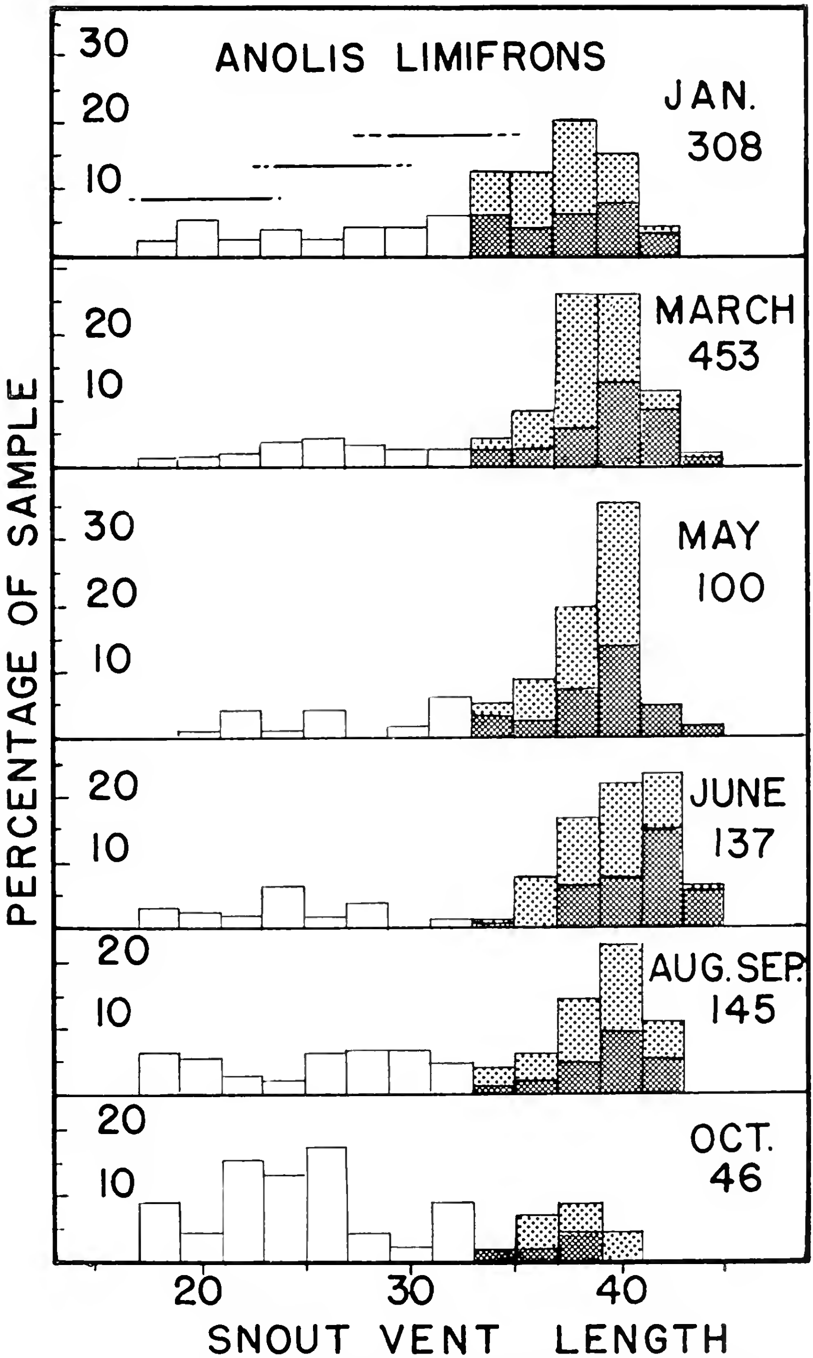

FIG. 5.—Population structure (Type 2) of *Anolis limifrons* at Beverly. Explanation as in Fig. 1.

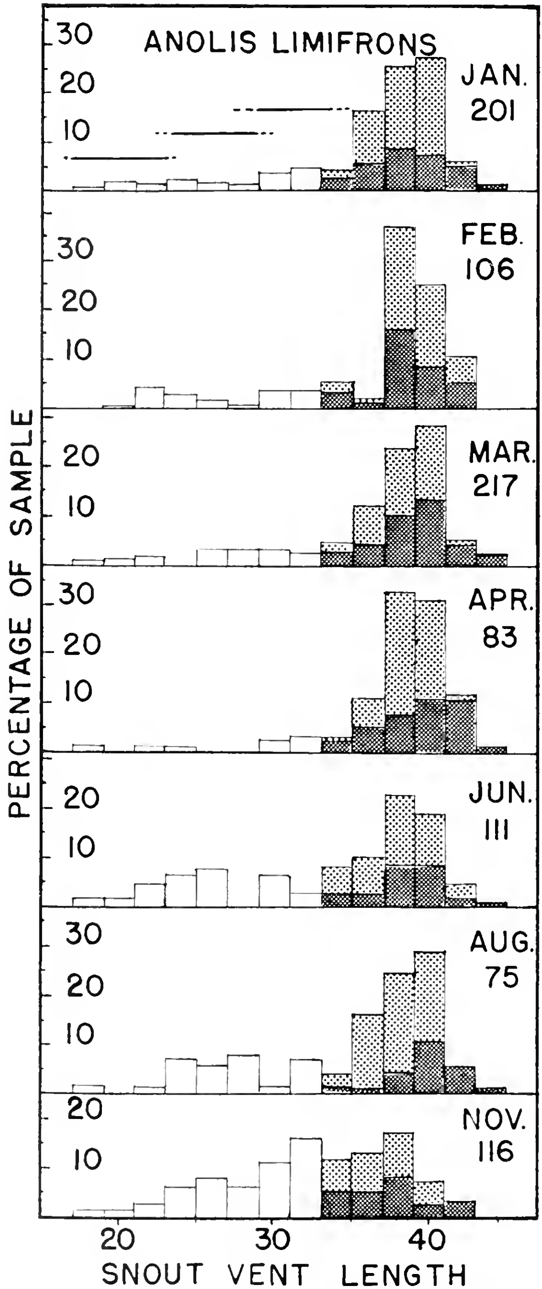

FIG. 6.—Population structure (Type 2) of *Anolis limifrons* at Turrialba. Explanation as in Fig. 1.

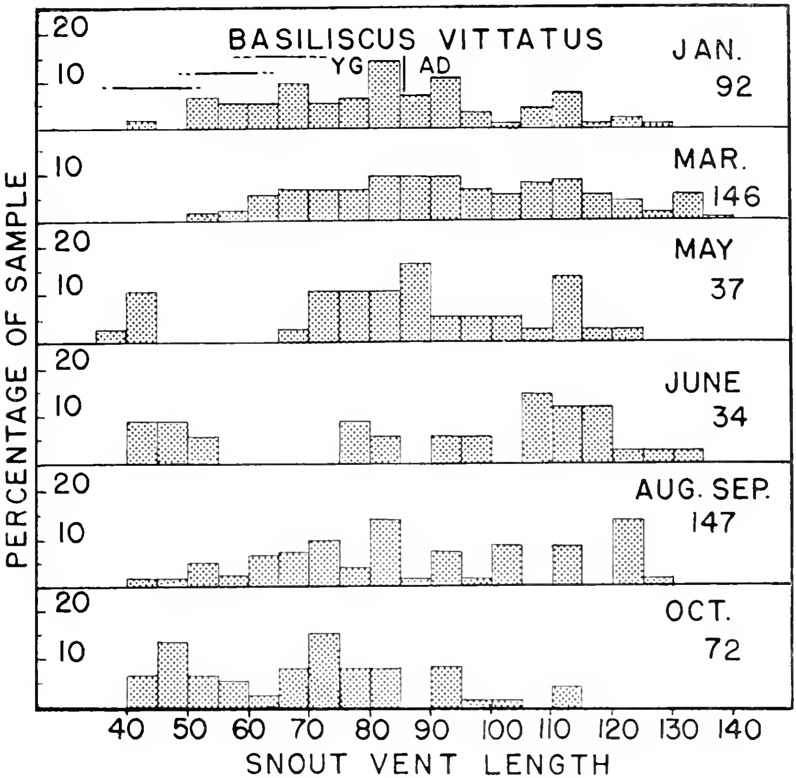

FIG. 7.—Population structure (Type 2) of *Basiliscus vittatus* at Portéte. Explanation as in Fig. 4, but with individuals grouped in 5-millimeter size classes.

northwest along the Caribbean Coast, Hirth (1963) found juveniles at all seasons but they were more abundant in August and September than they were earlier in the year. Hirth did not obtain samples in the late rainy reason when presumably juveniles would have been even more abundant.

Leiolopisma cherriei at Turrialba was found to undergo more pronounced seasonal changes than any of the species discussed above. Pooled samples from the drier part of the year, January through April, consist mostly of large adults; the few young present were well grown. From May through November the ratio of young increases (Fig. 8). At the end of the rainy season (November) and through the dry season (January to April) most adult females are nonreproductive or have only small ovarian follicles, whereas most have uterine eggs or large follicles from May through August. In general, the Caribbean lowlands have a warmer and wetter climate than Turrialba and egg-bearing females have been found in March

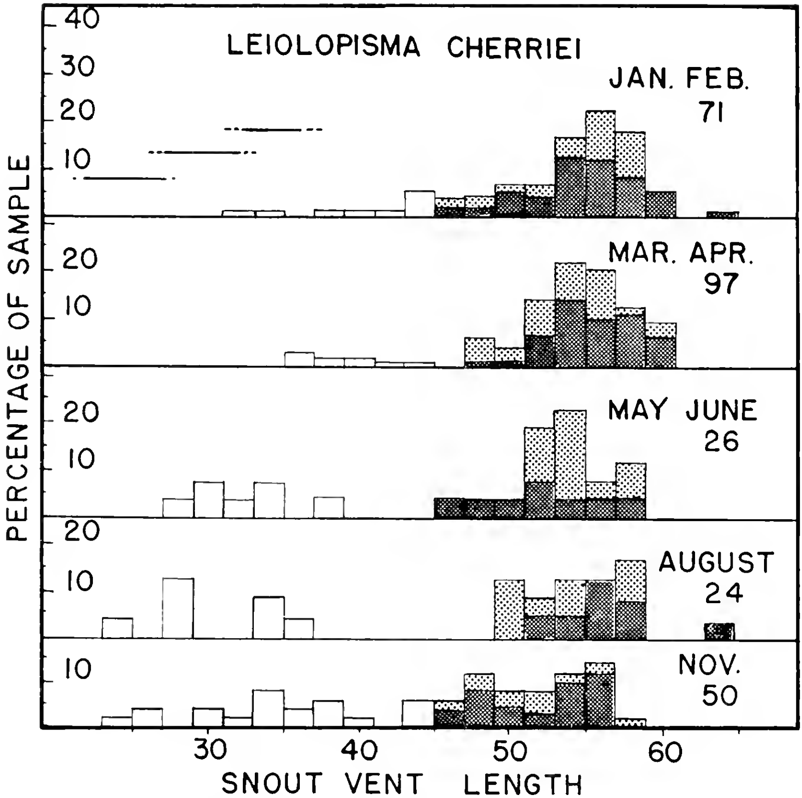

FIG. 8.—Population structure (Type 2) of *Leiolopisma cherriei* at Turrialba. Explanation as in Fig. 4.

(Greene, 1969; Fitch, 1973). No samples are available from the western part of Costa Rica, where seasonal constraints are probably greater than they are on the Caribbean versant. Perhaps this skink conforms to both type 2 and type 3 patterns in response to different climates in different parts of its range.

The Type 3 Population.—The type 3 population is characteristic of species that divide their annual cycle into an extended breeding season and a nonbreeding season of comparable length. The annual population cycle passes from a stage of relative homogeneity with only adults present at the beginning of the breeding season, to a heterogeneous stage at the end of the breeding season characterized by a mixture covering the full range from hatchlings to adults. Differences in lengths of breeding and nonbreeding periods, and the rapidity with which the young develop, result in notable differences between the kinds that have been assigned to type 3.

A type 3 pattern prevails in the parts of Costa Rica that have a severe dry season, the northwest (Guanacaste and northern Puntarenas provinces) and the Meseta Central including high and relatively dry parts of the Caribbean versant. In type 3, reproductive cycles correspond in general with the wetter half of the year. Individual females may produce eggs at regular intervals throughout the rainy season, but as the dry season sets in, production stops abruptly. Typically, all age groups from hatchlings to old adults are then present in the population but subsequently there are no increments of young for approximately half the year; hence, the youngest are arriving at adolescence as a new breeding season begins. Early in the breeding season the population consists largely of adults or adolescents, but young soon appear and become increasingly prominent; some may mature with sufficient rapidity to breed before the onset of the dry season. Some adults may survive through two breeding seasons or even more, but in most species there is a high percentage of population turnover from one year to the next. Population structure is continually changing in a predictable annual pattern.

Anolis cupreus conforms with type 3. It was studied at three lowland localities and one on the Meseta Central; the four populations show only minor differences in their seasonal trends. In December the population consisted of a mixture of all size groups but by March only adults were present. In summer a new crop of young appeared. At first their small size distinguished them from the adults; however by late autumn the size classes had merged. *Anolis intermedius* has a similar pattern (Fig. 9). It occurs at medium to high elevations on the Meseta Central and was sampled at San José. In a pooled sample (January-February from three years) there are individuals of nearly all sizes but few small juveniles. In samples from February-March and April-May, young are progressively fewer and larger, and in June there are only adults. In August-September there are adults and many hatchlings and juveniles but no young in later stages of growth. In November-December all sizes are represented, with a large majority consisting of immatures.

Cnemidophorus deppii conforms to the type 3 pattern, especially at Playas del Coco (Fig. 10). The samples from March, May, and July have progressively fewer young; only two of 89 are immature in July. In August hatchlings and juveniles are in evidence; November and December samples consist mostly of immature lizards. Samples from Boca de Barranca (Fig. 11) are notably different in having numerous juveniles in April, May and June-July as well as in August. This suggests that egg production continues through the dry season, although there is a reduction in the rate of production at that time of year. The dry season is somewhat less severe than at Playas del Coco. The Boca de Barranca samples are from the

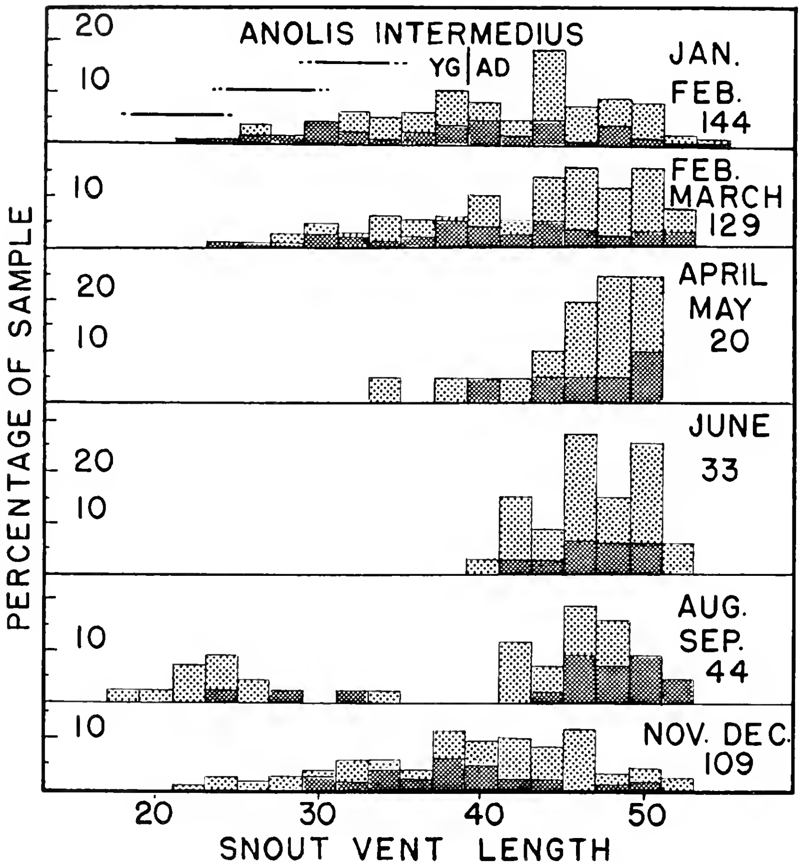

FIG. 9.—Population structure (Type 3) of *Anolis intermedius* at San José. Explanation as in Fig. 1.

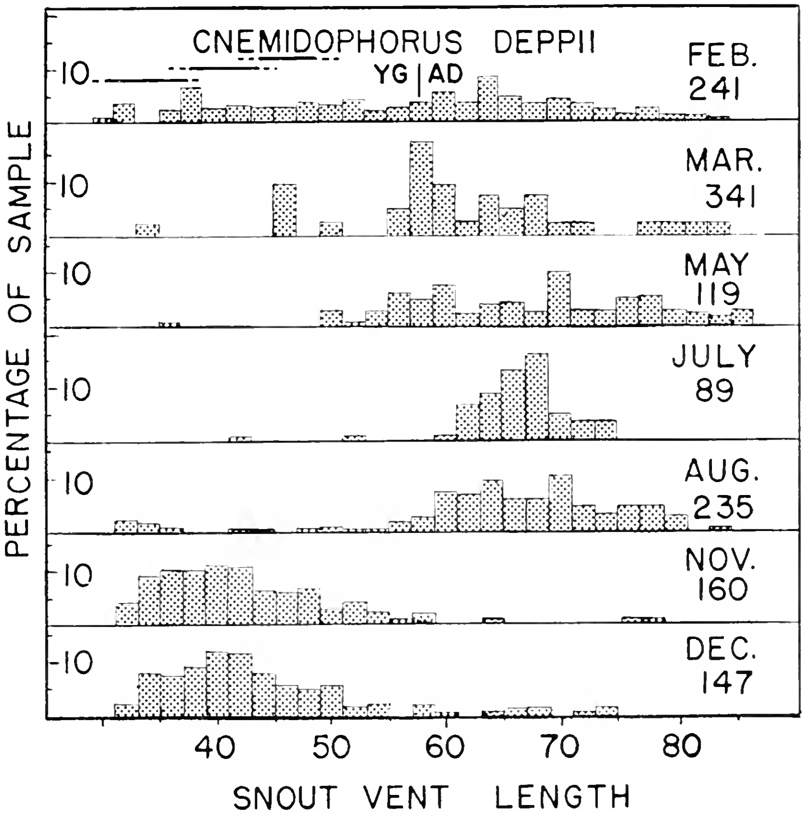

FIG. 10.—Population structure (Type 3) of *Cnemidophorus deppii* at Playas del Coco. Explanation as in Fig. 4.

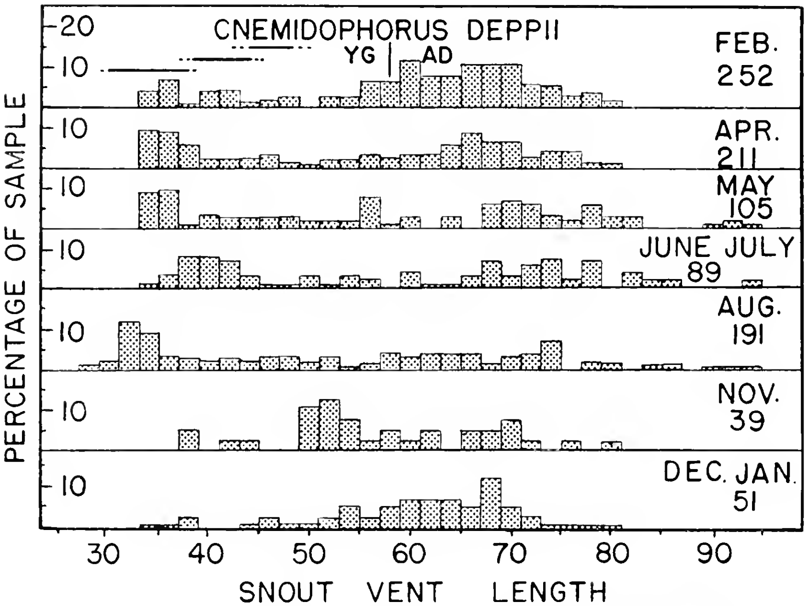

FIG. 11.—Population structure (Type 3) of *Cnemidophorus deppii* at Boca de Barranca. Explanation as in Fig. 4.

grounds of the Marbella Hotel where flower beds and yards are regularly sprinkled in the dry season. Perhaps in this small area the sprinkling partially nullified the effects of the dry season by providing drinking water, damp sand for oviposition, and a concentration of insect food.

Sceloporus variabilis at Playas del Coco and Boca de Barranca is fairly typical of a type 3 pattern. At Boca de Barranca (Fig. 12) samples from February, April, May and June-July consist mostly of adults. There are young of various sizes in February but they become fewer and larger as the dry season progresses, with no further increments of hatchlings. Average size of sexually mature individuals also increases during the dry season. In August a new crop of hatchlings appears. By November and December, the population consists mainly of young, the largest already overlapping in size

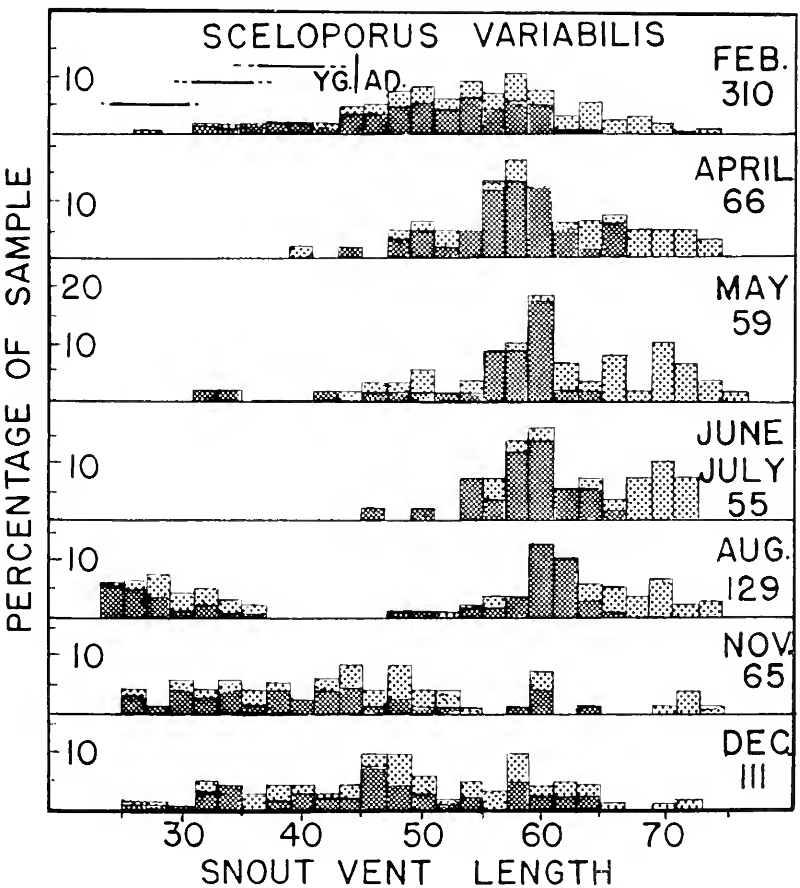

FIG. 12.—Population structure (Type 3) of *Sceloporus variabilis* at Boca de Barranca. Explanation as in Fig. 1, but sex is indicated in all sizes.

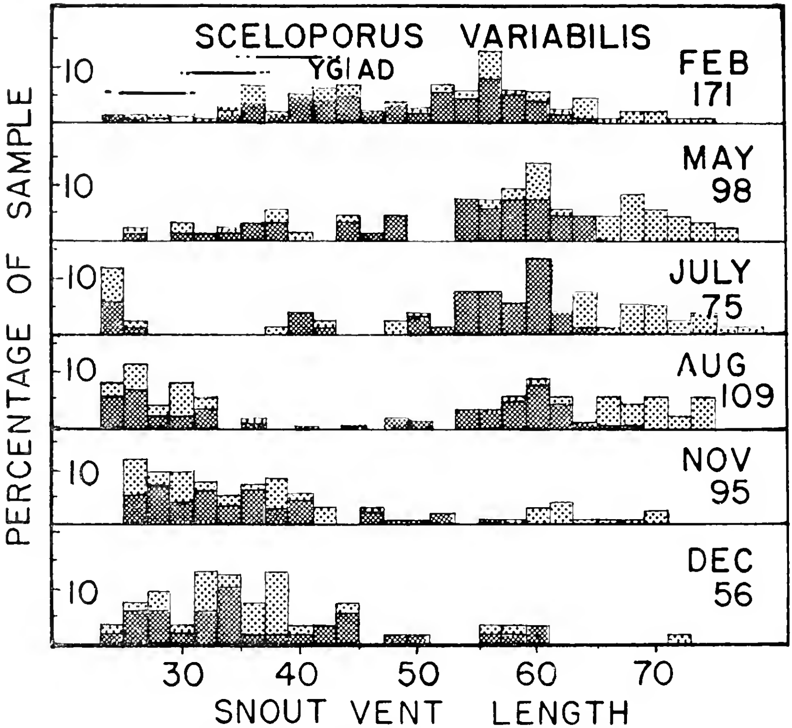

FIG. 13.—Population structure (Type 3) of *Sceloporus variabilis* at Playas del Coco. Explanation as in Fig. 1, but sex is indicated in all sizes.

the preceding generation. At Playas del Coco (Fig. 13) the trend is similar but not so well defined. In May there are more young, some still near hatchling size. This would seem to indicate production of eggs even in the dry season. The summer hatchlings appear in early July, before they are present at Boca de Barranca.

Basiliscus basiliscus fits the type 3 pattern poorly. In this large, semi-aquatic lizard, population parameters are much affected by local conditions in different streams. Regardless of the time of year every population sample obtained had a high proportion of immature individuals (Fig. 14). In each sample these immatures tend to be concentrated in one or two dominant size classes representing relatively brief periods of concentrated and successful reproductive activity; these periods do not correspond closely between different localities, or between different years at the same locality. Amount and distribution of precipitation is critical.

Although *Sceloporus malachiticus* most nearly conforms with a type 3 pattern, it is unique in some respects (Fig. 15). Samples from Cartago and San José were pooled; these localities are 19 km apart

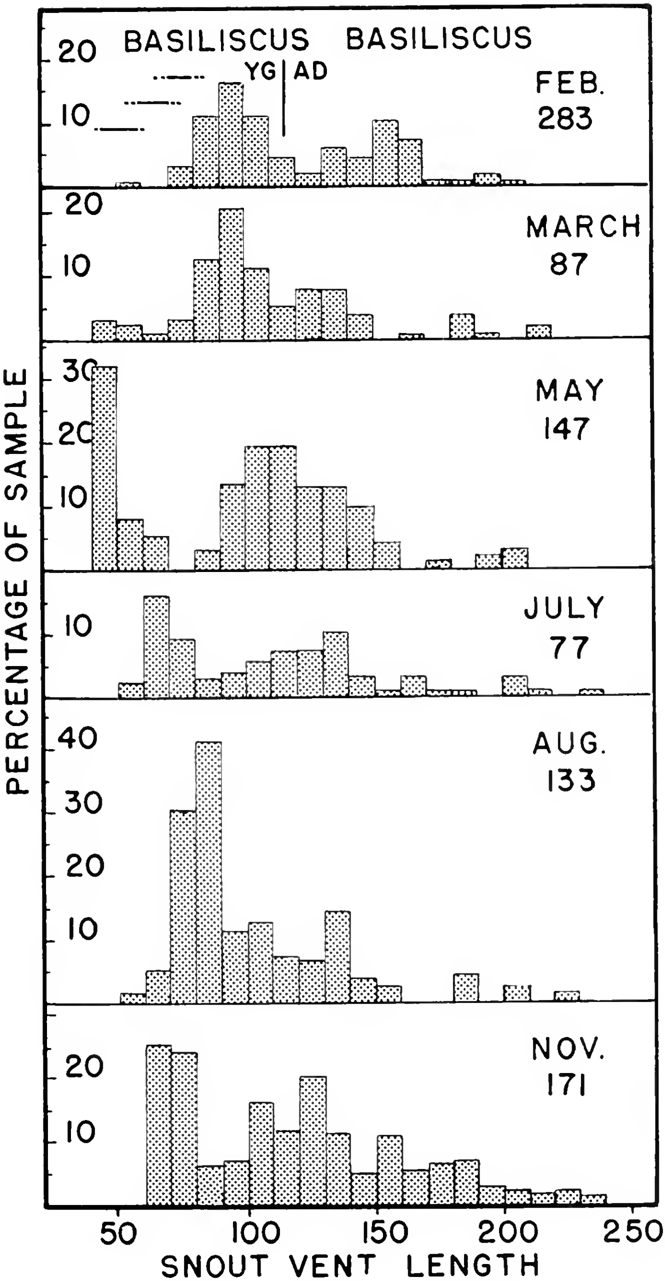

FIG. 14.—Population structure (Type 3) of *Basiliscus basiliscus* at Finca Taboga, Río Higuerón. Explanation as in Fig. 4, but with individuals grouped in 10-millimeter size classes.

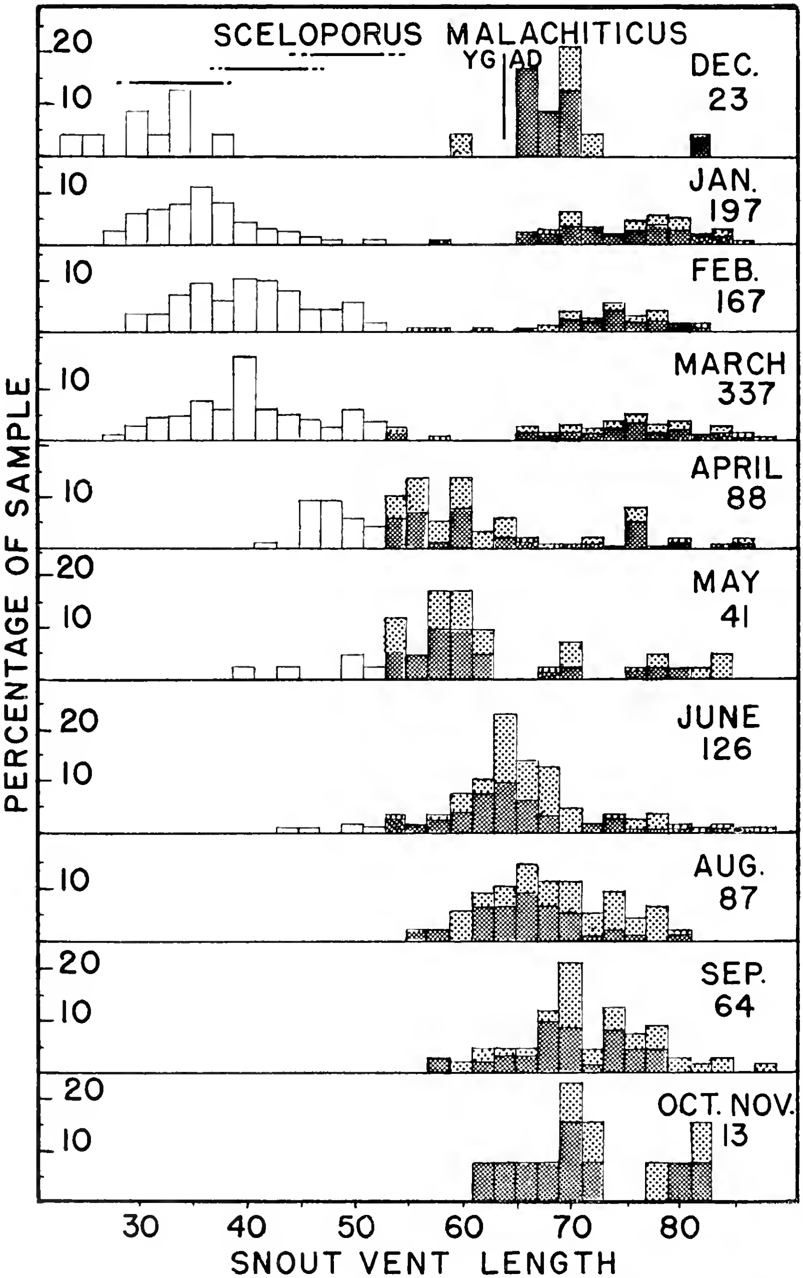

FIG. 15.—Population structure (Type 3) of *Sceloporus malachiticus* as shown by combined samples from Cartago and San José. Explanation as in Fig. 1.

and separated by the continental divide. Cartago has a slightly cooler and drier climate, but seasonal trends in *S. malachiticus* populations seem to correspond closely enough at the two localities to justify combination of the samples. In the dry season there is no reproductive activity. When the rainy season starts in April and May, ovarian follicles begin to enlarge and ovulation occurs in summer (Marion and Sexton, 1971). This lizard is viviparous, and gestation is prolonged, with births occurring in December and January. Females produce only one litter annually. In winter the recently born juveniles constitute a large part of the population. By late spring their cohort has grown sufficiently to overlap adults in size. Through the summer and autumn months, juveniles are scarce. Nearly all females are gravid in summer but a few retarded young fail to gain maturity until late in the summer.

At higher altitudes, with relatively low temperature, less insolation, and a less severe dry season, the seasonal pattern indicated by figure 15 is not developed. Growth is delayed, so that females are usually somewhat more than a year old when they produce their first litters and births are scattered throughout the year.

Although *Gonatodes albogularis* has a type 1 pattern in the Caribbean lowlands, it conforms to a type 3 pattern at Boca de Barranca, where there is a seasonally dry climate (Fig. 16).

The Type 4 Population.—The type 4 population is most familiar to investigators because it occurs in those kinds of lizards that penetrate farthest into the temperate zone, and live in areas having a long, severe winter and a short growing season. There is a short annual breeding season resulting in production of a cohort of young which usually require more than one year to mature. Consequently the population is structured with several discrete annual age groups, one or more of which consist of immatures that do not participate in the breeding season. Surprisingly, type 4 populations occur in the tropics and even in the relatively uniform climate of rain forests, as well as in northern areas.

I found type 4 populations only in the large iguanines, *Ctenosaura similis* and *Iguana iguana*, and I did not obtain adequate population samples of the iguana. However, both of these lizards have a short annual breeding season, and the young mature late in the second year at the earliest. Data from pooled samples of *Ctenosaura similis* from various localities in western Costa Rica show that after the annual crop of eggs hatches in spring there are two distinct size groups of young, hatchlings and yearlings (Fig. 17). The former grow more rapidly and by late autumn they overlap the yearlings in size. The samples available for the iguana are smaller and less well distributed, but indicate that the iguana follows a similar pattern. The occurrence of hatchlings and the distribution of dates of egg-laying indicates that the breeding sea-

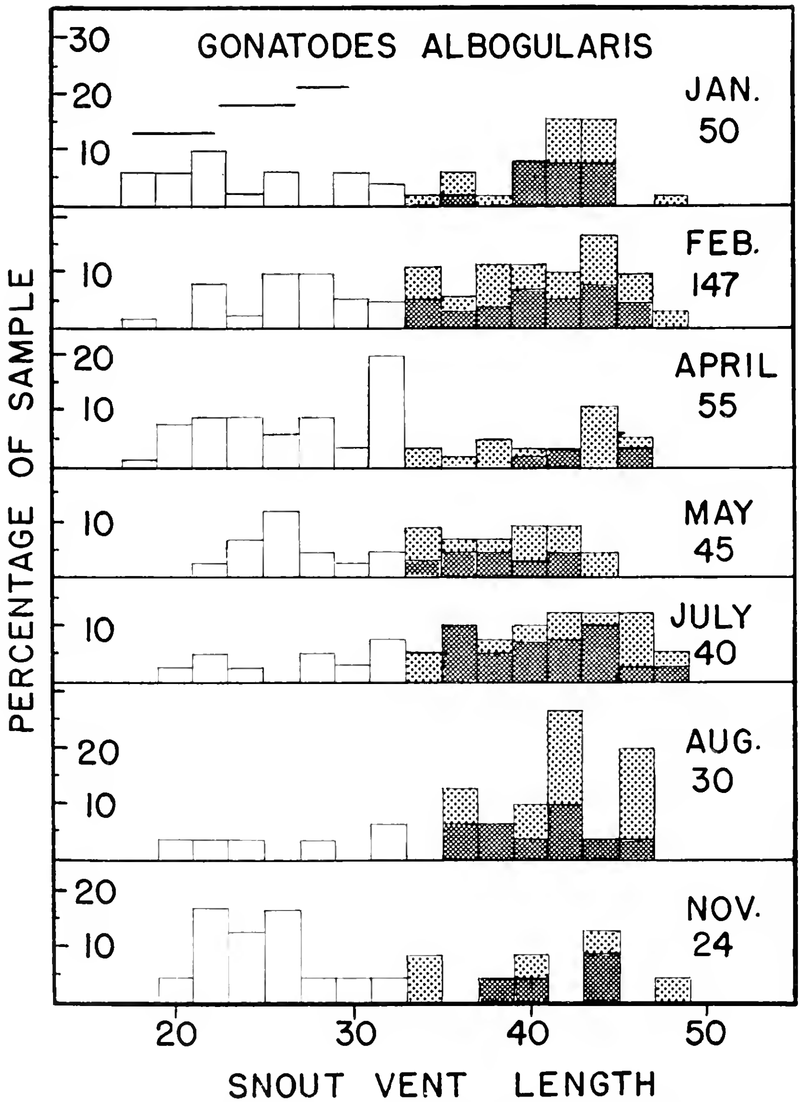

FIG. 16.—Population structure (Type 3?) of *Gonatodes albogularis* at Boca de Barranca. Explanation as in Fig. 1.

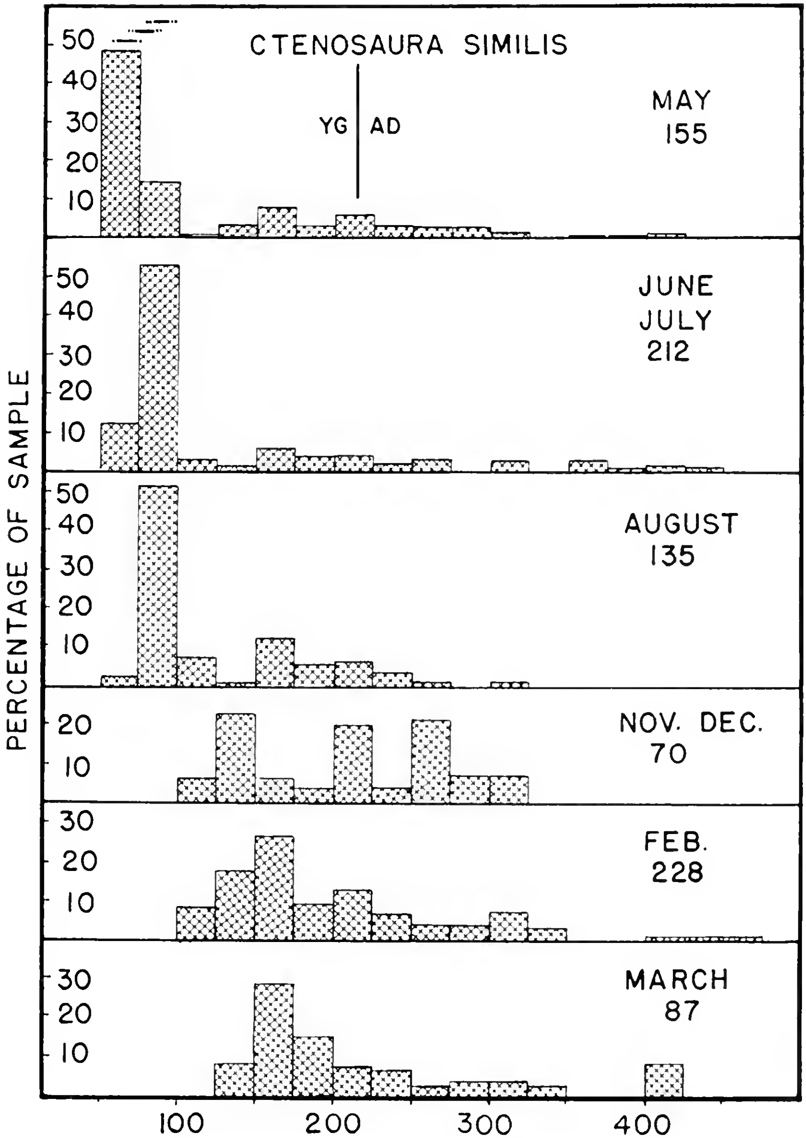

FIG. 17.—Population structure (Type 4) of *Ctenosaura similis* in Guanacaste and Puntarenas provinces. Explanation as in Fig. 4, but with individuals grouped in 25-millimeter size classes.

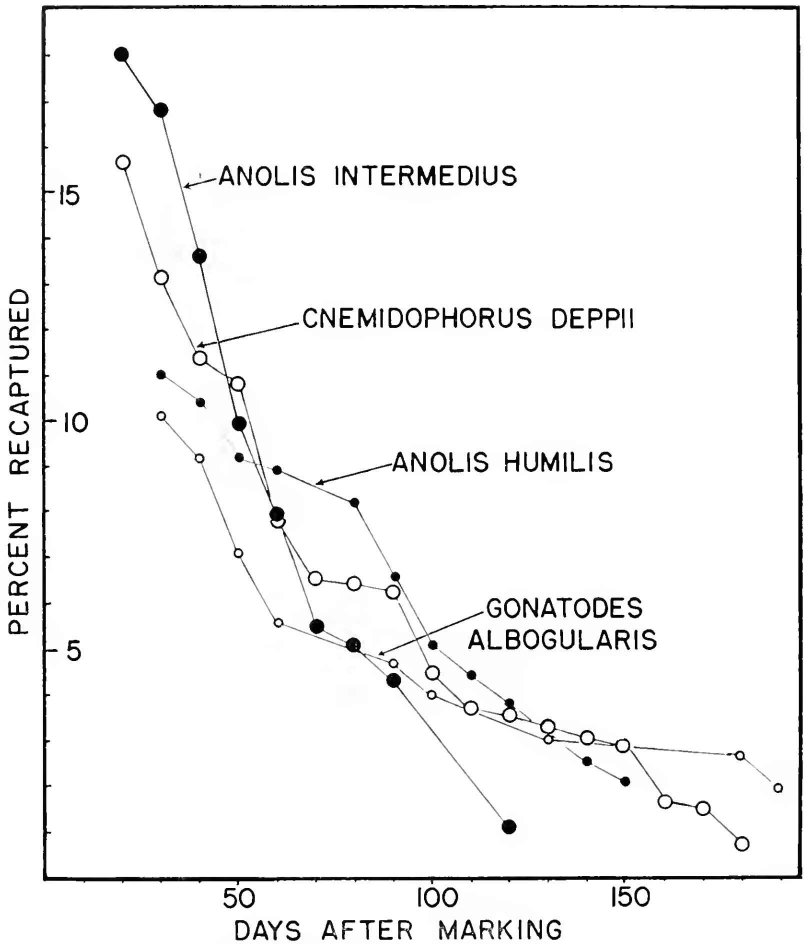

FIG. 18.—Cumulative percentages of marked lizards of four species recaptured indicating trends of survivorship.

son is somewhat less restricted than in the ctenosaur, with the possibil.ty that individual females lay more than one clutch in the course of a season. Iguanas are restricted to warm lowlands, but occur both in seasonally dry areas and those that are humid. In the latter they are exceptional in having a breeding season limited to a short part of the year.

Survivorship.—Under natural conditions longevity differs greatly among the many kinds of lizards studied, and is not closely correlated with the types of seasonal schedule and population structure described above. Although the 29-month span of my field work was long enough to yield significant information about longevity, drastic disturbance of nearly all the study areas (e.g., tree-cutting,

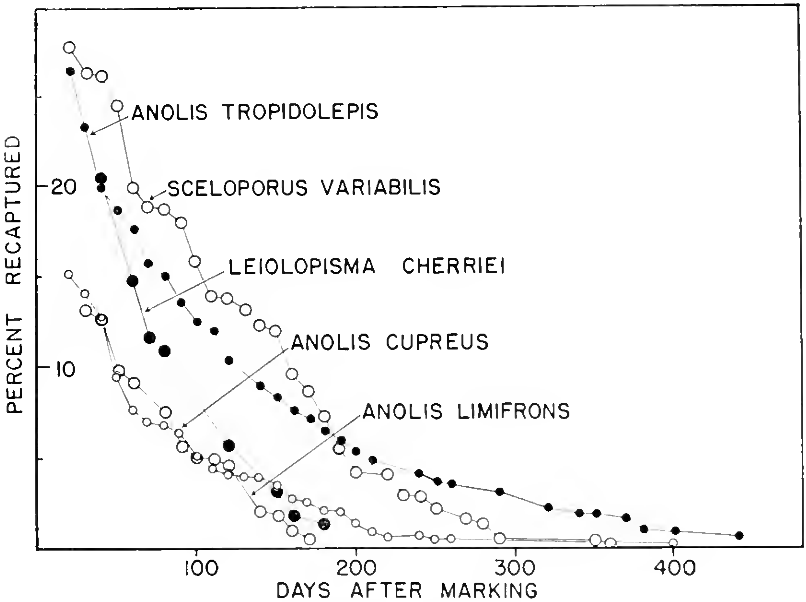

FIG. 19.—Cumulative percentages of marked lizards of five species recaptured after varying intervals, indicating trends of survivorship.

bull-dozing, flood, or unusually high tide) prevented the lizards from surviving as long as they would have in undisturbed habitats; some populations were more drastically affected than others. Figures 18 and 19 show rates of disappearance of the marked individuals of several species from the study areas and perhaps provide the basis for a rough comparison of their mortality rates.

In the smaller anoles (*Anolis limifrons*, *A. humilis*, *A. intermedius*) and in *Ameiva quadrilineata*, *Cnemidophorus deppii* and *Sceloporus variabilis*, sexual maturity is attained at an age of four to six months. Population turnover is extremely rapid, and the records suggest that individuals rarely if ever survive through two full breeding seasons. In *Gonatodes albogularis*, *Sceloporus malachiticus*, and especially in the montane *Anolis tropidolepis*, maturity is delayed until late in the first year, population turnover is somewhat slowed, and longevity is greater. In the basilisks, large size and delayed maturity are correlated with even slower population turnover. Seemingly the mortality rate is high in young, but adults are relatively safe. Adults are exceedingly elusive, especially those of *Basiliscus basiliscus*, but some individuals of both species were captured and marked. In the late stages of the field work individuals of both species (mostly *B. vittatus*) that could not be caught alive were shot. These were found to include individuals marked soon after the beginning of field work, and they revealed that in *B. vittatus* at least, normal life expectancy is much greater than in any of the smaller kinds of lizards studied (Table 1). *Ctenosaura similis* might be expected to have even greater longevity than *Basiliscus* because of its large size and delayed maturity. However, adults are too wary to be caught and marked except on a few occasions and nothing was learned of longevity.

DISCUSSION

In a pioneer study, Baker (1947) demonstrated that in tropical rain forest of Espirítu Santo in the New Hebrides there is well defined seasonality in the skink *Emoia cyanura.* Espirítu Santo lies at 15° 15′ south latitude; day length, precipitation and temperature change little throughout the year. Although breeding occurs throughout the year, its level changes markedly from a peak in the warmest part to a trough at the opposite extreme when temperature averages only 2°C lower. Thus these lizards are highly sensitive to changes in the physical environment and respond in the level of their reproductive activity. Many later studies of local lizard populations in a variety of tropical environments have extended these findings. In general, such investigations have shown that tropical lizards often have long breeding seasons, but that year-round reproduction occurs only in rain forest and even there the level of reproduction tends to be positively correlated with the amount of precipitation. Elsewhere, in regions of seasonal drought, the breeding season tends to correspond with the wet season; reproduction ceases or declines to a relatively low level in the dry season. Seasonal interruption of reproduction, or reduction in its level results in changing population structure, with certain age groups either missing or less well-represented than both older and younger groups.

In their investigation of evolutionary strategies in the reproduction of lizards, Tinkle, Wilbur, and Tilley (1970) compiled data from the literature on 27 tropical species along with a larger number of kinds from temperate regions. They stated, "Lizards are clearly divided into two strategies: early-maturing, multiple-brooded vs. late maturing, single-brooded. . . ." Contrasting the tropical species with the temperate, they found in the former: larger average

TABLE 1.—Survivorship in Marked Lizards of Various Species

Species	Marked in 1967-68	Recaptured > 6 mos.	Recaptured > 12 mos.	Recaptured > 18 mos.	Recaptured > 24 mos.
Sceloporus variabilis	604	70(11.6%)	0	0	0
Anolis humilis	305	6(1.9%)	1(.33%)	0	0
Anolis cupreus	1482	48(3.24%)	3(.20%)	0	0
Anolis tropidolepis	316	27(8.45%)	7(2.22%)	0	0
Basiliscus vittatus	90	6(6.66%)	4(4.45%)	2(2.22%)	2(2.22%)

size at sexual maturity, larger adult female size, slightly smaller number of eggs per clutch, and a higher ratio of oviparous to viviparous species. Of the 15 tropical species discussed here, only one, *Ctenosaura similis,* is late-maturing and single-brooded, whereas nine are early maturing and multiple-brooded. The other four are somewhat intermediate; the viviparous *Sceloporus malachiticus* is single-brooded, and *Basiliscus basiliscus, B. vittatus* and *Anolis tropidolepis* have somewhat delayed maturity. As to size, most of the 15 species are small, but the average is raised by the relatively gigantic *Ctenosaura similis* and also by the two species of *Basiliscus.* With few exceptions, the number of eggs is small. The clutch consists of only one egg in the six species of anoles and the gecko, *Gonatodes albogularis.* In the two teiids and the skink, the average clutch size is between 2 and 3. The average clutch size is 3.0 in *Sceloporus variabilis,* 3.9 in *Basiliscus vittatus,* 4.6 in *Sceloporus malachiticus,* 6.0 in *Basiliscus basiliscus.* Only *Ctenosaura similis* has large clutches of more than 20 eggs. Of the 15 species, only *Sceloporus malachiticus* is viviparous; of the 58 species of lizards recorded from Costa Rica, there are only three that are known to be viviparous.

Tinkle, *et al.* (1970) noted the absence of a significant correlation between clutch size and body size at maturity in tropical lizards. However, such correlation definitely does exist in the 15 species that I investigated. Doubtless the lack of correlation found by Tinkle *et al.* resulted, at least in part, from the fact that insular species (having few natural enemies and reduced clutch size) were included along with mainland kinds. Also, their list included species of *Draco,* which parallels *Anolis* in specialization for an active, arboreal existence, including reduction in clutch size. If the insular species and the species of *Draco* are excluded, the remaining 12 examples of Tinkle *et al.* do show high correlation of body size and number of eggs per clutch.

A much different combination of ecological traits from those hypothesized for tropical lizards by Tinkle *et al.* (1970) would be expected from concepts of selection proposed or developed by Dobzhansky (1951), MacArthur and Wilson (1967), Pianka (1970) and also MacArthur (1972). They recognized two basic types of selection to which populations are subject, depending on the type of environment. "*K*-selection" is most characteristic of environmental type best exemplified by a tropical rain forest. In this type, physical factors are relatively benign and stable. Weather is predictable. The populations of a given organism tend to be stable, and often in equilibrium near the carrying capacity. Interspecific and intraspecific competition is usually keen, and mortality is density-dependent. Animals are highly adapted to their communities and are "fit" so that they have notable longevity, with slow development, delayed maturity, large body size, few young per clutch, repeated reproduction and parental care (occasionally expressed in viviparity). Conversely, "*r*-selection" is most characteristic of an environment typified (in extreme form) by an Arctic tundra. There, environmental conditions are unstable and often harsh. Weather is subject to extremes, which may bring about catastrophic decimation of animal populations in a density-independent fashion. As a result populations are unstable, are often below the carrying capacity, and competition may be lax. Selection favors a short life span, rapid development, early maturity, small size, energy channeled into a single, early reproductive effort, with a large number of offspring, and lack of parental care.

Most terrestrial environments fall somewhere between these two extremes. Presumably the assemblage of tropical lizard species dealt with in the present study represents environments that are most likely to show *K*-selection. Table 2 is designed to test conformity of each species with the two types of selection on the basis of eight separate criteria. A species that conformed with *r*-selection in all respects would have a rating of 8, one that conformed with *K*-selection would have a rating of 24 and one that was intermediate would have a rating of 16. Assuming that the criteria used are appropriate and that the ratings have been made correctly, it appears that none of the species conforms entirely with either type, but that 12 of the 15 fit *r*-selection better than *K*-selection.

"Coarse-grained" and "fine-grained" environments have been recognized by several recent authors as producing different types of selection, the latter permitting more specialization and closer adaptation. According to Levins (1968) a species "loses fitness in a heterogeneous environment. It would be better off specialized, but the uncertainty of the environment forces niche expansion." Compared on this basis, the 15 species of this study seem to have members in each type of environment and some that are intermediate. *Basiliscus basiliscus* is perhaps the best example of a species living in a coarse-grained environment. Within the area where it occurs it is not generally distributed but is limited to watercourses and their vicinity, and along them it is irregularly distributed with concentrations where there are log jams, uprooted large trees, or undermined banks with dense thickets. These alternating features are accentuated by seasonal change; a stream that is a rushing torrent during the rainy season may be reduced to a series of puddles in the dry season, and the log jams and thickets that are used as shelter may be drastically altered or swept away completely in time of flood. *Basiliscus vittatus* and *Anolis lionotus* are also streamside species subject to some of the same coarse-grained features. *Ctenosaura similis* and *Sceloporus malachiticus* are usually associated with irregularly distributed environmental features such as rock outcrops, buildings, or hollow trees, and their

TABLE 2.—*r*-selection and *K*-selection in Some Costa Rican Lizards

	Size (S-V in mm) 1=35-60 2=70-150 3=300 or more	Time to maturity in mos. 1=3-5 2=6-10 3=more than 12	Sexual dimorphism 1=size and color 2=color and/or display organ 3=little or none	Number of eggs or young 1=7 or more 2=3-6 3=1 or 2	Number of broods 1=5 or more 2=2-4 3=1	Population turnover 1=1 year 2=1-2 years 3=more than 2 yrs.	Habitat stability 1=seral 2=intermediate 3=stable	Habitat uniformity 1=coarse 2=intermediate 3=fine	Selection rating $r=8$ $K=24$
Ameiva quadrilineata	2	2	1	3	2	1	1	1	13
Anolis cupreus	1	1	1	3	1	1	2	2	12
Anolis humilis	1	1	2	3	1	1	3	2	14
Anolis intermedius	1	1	2	3	1	1	2	2	13
Anolis limifrons	1	1	2	3	1	1	2	2	13
Anolis lionotus	1	1	2	3	1	2	2	1	13
Anolis tropidolepis	1	2	2	3	1	2	3	3	17
Basiliscus basiliscus	2	2	1	2	2	3	1	1	14
Basiliscus vittatus	2	2	1	2	2	3	1	1	14
Cnemidophorus deppii	1	1	1	2	2	1	1	1	10
Ctenosaura similis	3	3	1	1	3	3	2	1	17
Gonatodes albogularis	1	1	1	3	1	2	3	3	15
Leiolopisma cherrici	1	2	3	3	2	2	3	2	18
Sceloporus malachiticus	2	2	1	2	3	2	2	1	15
Sceloporus variabilis	1	1	1	2	2	1	1	1	10

environments are likewise coarse-grained. In contrast the species of leaf litter in rain forest (*Anolis humilis, Leiolopisma cherriei*) or those of tree-trunks (*Gonatodes albogularis, Anolis tropidolepis*) have fine-grained environments. Again, there is no definite correlation between these environmental types and population structure or survivorship.

CONCLUSIONS

Four types of population structure were found to result from the varying climates and reproductive strategies in the 15 species of tropical lizards studied in Costa Rica. Type 1 is a stable population with all ages constantly represented, from the most numerous and youngest to the relatively scarce oldest lizards; type 2 also has all age groups constantly present, but their ratios are constantly changing, with an older group sometimes better represented than a younger one reflecting fluctuation in the level of reproduction. Type 3 results from seasonality of breeding, and changes throughout the annual cycle, from relative homogeneity (with all adults) to heterogeneity with immatures of all sizes as well as adults. Type 4 consists of a structured population of many successive annual cohorts, and results from a short annual breeding season and delayed maturity, paralleling trends in the kinds of lizards that occur farthest from the equator.

Small body size, rapid population turnover, frequent reproduction, oviparity, small clutch-size, type 2 or 3 population structure, and sexual dimorphism (in color or display organs or body size or all three) are characteristic of the populations studied with few exceptions. Although occurring in communities that would be expected to have mainly *K*-selection, the species do not conform consistently to the criteria expected in products of *K*-selection. The majority of the species fit better with the criteria of *r*-selection, but each species shows some mixture of the two sets of traits, and no two species are alike in this respect.

In contrast with lizard populations of the temperate zones, those of the tropics are less restricted to seasonal schedules. Living in more constant environments, they are able to distribute their activities, such as those concerned with reproduction, over a greater part of the annual cycle. The iguanid anoles and the sphaerodactyline geckos, two groups that are highly successful in the Neotropical region, have progressed farthest in this regard; in rain forests and cloud forests their reproductive effort is uniformly distributed over the entire year. The female lays one egg at a time, the left and right ovaries alternating, so that, usually carrying two eggs in different stages of growth, she is not much handicapped and continues her normal activities. Aside from its various other implications, the one-egg clutch may be regarded as an extreme specialization for an active way of life. Each egg may be left in a different place (though both groups are known to use communal nests at times). Eggs are deposited in damp sheltered places, but are not buried in special nest burrows.

Therefore production of eggs and oviposition involve a minimum of stress. Dispersal of eggs in time and space provides security from: a) catastrophic events such as flood or drought which might catch the eggs or young at a vulnerable stage, b) concentrated predation, c) intense intraspecific competition for food and space, such as might occur when many young emerge simultaneously from the same nest.

Climates in the tropics that have strong seasonality impose annual cycles on their lizard populations. In areas that have a severe dry season, the lizards' annual cycles are comparable with those that occur in species of the temperate zones except that there is no hibernation period. There is a breeding season of varying length but confined to one part of the year and presumably adjusted to avoid the worst rigors of the year-round climate and exploit the benefits, such as adequate moisture for the incubating egg, and an abundant supply of suitable food (usually insects) for the breeding adults and/or the hatchlings. Even in the wet climate of the Caribbean lowlands some lizards, especially those of seral situations, such as *Anolis limifrons*, *Basiliscus vittatus* and *Leiolopisma cherriei* alter the level of their reproductive activity in response to wetter or drier weather at certain times of year. In general, heavy precipitation is correlated with heightened reproduction, whereas drought is correlated with slowing or cessation of reproductive activity.

The long and severe dry season of western Costa Rica (Guanacaste and northern Puntarenas provinces, where monthly precipitation in December, February, March, and early April is usually less than 25 mm) limits reproduction mainly to the wetter half of the year in most species. An extreme case is *Ctenosaura similis* which is limited to a short and concentrated breeding season, with large clutches of eggs, relatively small hatchlings, and delayed maturity as facets of its reproductive strategy. In ctenosaurs, the young differ from adults in their behavior, microhabitats (Henderson, 1973), size and type of food items (Montanucci, 1968) hence intraspecific competition is minimized. In *Basiliscus basiliscus*, *Iguana iguana* and *Anolis cupreus* there is a less well-defined segregation of young and adults.

SUMMARY

Free-living populations of 15 species of lizards were studied at 14 localities in Costa Rica; the study sites include a wide range of altitudes, habitats and climates. Mark and recapture studies were

carried out over a three-year period for most of the species. At most of the localities two or more species were studied simultaneously; thus the results provide a basis for both intraspecific and interspecific comparisons.

Unlike lizards of the Temperate Zone, the tropical species included in this study all are active throughout the year; however most of them show some seasonality in their annual cycles. Their different population structures result largely from the timing of reproduction and rate of development and survivorship of the cohorts of young produced. In some kinds, population structure changed markedly in response to seasonal changes in the weather. Recognizable components of individual populations were adult males and females, and immatures at various stages of development. Snout-vent length is highly correlated with age in immatures; there is less correlation in adults because growth continues after attainment of maturity.

On the basis of their population structures, reproduction and survivorship, the species studied can be arranged in a graduated series from those of small size, early maturity, high production, and rapid turnover, to those that are large and have delayed maturity, low production and slow turnover. Four fairly distinct but overlapping types of population structure can be recognized within this range. Type 1 is confined to climates lacking seasonal contrast and results from year-round reproduction at a uniform level. The population structure is stable and includes individuals of all ages in unchanging ratios. This type is best exemplified by *Anolis tropidolepis* of montane cloud forest, and less perfectly by *A. humilis*, probably *A. lionotus*, and by *Gonatodes albogularis*, all of the Caribbean rain forest. Type 2 also has year-round reproduction with all ages represented in the population at all times, but the level of reproduction and the ratios of different age groups undergo constant seasonal change. This type occurs in wet climates that have moderate seasonal change and was found developed to various degrees in *Ameiva quadrilineata*, *Anolis limifrons*, *Basiliscus vittatus*, and *Leiolopisma cherriei*. Type 3 is characteristic of areas having a long dry season, where lizards generally confine their reproduction to the wetter part of the year. At the beginning of the breeding season the population consists essentially of reproductive adults, but subsequently successive increments of young are added until all classes from hatchlings to adolescents are found along with the adults (by then reduced to relatively low numbers) at the end of the breeding season. Type 3 prevails in northwestern Costa Rica and was found in *Anolis cupreus*, *A. intermedius*, *Basiliscus basiliscus*, *Cnemidophorus deppii*, *Gonatodes albogularis*, *Sceloporus variabilis* and *S. malachiticus*. The latter species is transitional to type 4 which otherwise was found only in the large iguanid

Ctenosaura similis. In type 4 there is a relatively short annual breeding season and delayed maturity resulting in a sharply structured population that consists of several or many discrete annual age groups at least two of which are immatures.

Survivorship was judged from the rate at which marked individuals disappeared from the populations on the small study areas, but some of the turnover was caused by shifts of individuals and this spatial displacement could not be evaluated accurately. In most species, population turnover was rapid, with most individuals replaced in the course of a year. It was especially rapid in the smaller species of anoles, in *Cnemidophorus deppii, Ameiva quadrilineata* and *Sceloporus variabilis.* In contrast to these species the montane *Anolis tropidolepis* and the two species of basilisks are notably longer lived and individuals often survive for more than a year. *Ctenosaura similis* clearly is in a class by itself surviving longer than any of the smaller kinds of lizards studied.

Previous findings and predictions about populations of tropical lizards are partially borne out by the present findings. Conforming with trends indicated by Tinkle *et al.* (1970), most of the tropical lizards included in this study have relatively small clutches, and have a low ratio of viviparous to oviparous kinds compared with some from the temperate zone. However, the lack of correlation between size of female and number of eggs per clutch reported by Tinkle *et al.* is not borne out. Most of the species were found to conform to the strategy of early maturity and multiple broods. Only one of the 15, *Ctenosaura similis,* definitely conforms to the opposite strategy of late maturity and single broods. Appraised by some of the main criteria of *r*-selection and *K*-selection, no species of the 15 is fully committed to either type; instead all are intermediate in some degree, with a majority favoring *r*-selection.

RESUMEN

Poblaciones salvajes de 15 especies de lagartos fueron estudiadas en 14 localidades en Costa Rica; los lugares de estudio incluyen un amplio rango de altitudes, habitats y climas. Estudios de marca y recaptura fueron llevados a cabo por un período de tres años para la mayoría de las especies. En la mayoría de las localidades dos o más especies fueron estudiadas simultáneamente; por lo tanto los resultados proporcionan una base para comparaciones intraespecíficas e interespecíficas.

A diferencia de los lagartos de las zonas templadas, las especies tropicales incluidas en este estudio son activas durante todo el año; sin embargo, casi todas muestran periodicidad en sus ciclos anuales. Las diferentes estructuras de las poblaciones resultan mayormente de la regulación del tiempo de reproducción y la tasa de desarrollo y sobrevivencia de las cohortes de jóvenes producidas. En algunos tipos la estructura de las poblaciones cambiaba marcadamente en respuesta a cambios periódics en el clima. Componentes reconocibles de poblaciones individuales fueron machos y hembras adultos, e inmaduros a varios niveles de desarrolo. La distancia (cabeza-tronco) está altamente correlacionada con la edad en los inmaduros; hay menor correlación en los adultos porque el crecimiento continua despues de la madurez.

En base a las estructuras de sus poblaciones, reproducción y supervivencia, las especies estudiadas pueden ser agrupadas en una serie gradual de aquellos de tamaño pequeño, temprana madurez, alta producción, y rápido reemplazo, a aquellos que son grandes, y que tienen madurez tardía, baja producción y reemplazo lento. Cuatro tipos de estructuras de poblaciones bastante diferenciables pero sobreponibles pueden ser reconocidas en este rango. El tipo 1 está confinado a climas sin contrastes de estaciones y resulta de reproducción durante todo el año a un nivel uniforme. La estructura de la población es estable e incluye individuos de todas las edades en proporciones invariables. Este tipo está bien representado por *Anolis tropidolepis* de selvas nubladas de montaña, y menos perfectamente por *A. humilis*, probablemente *A. lionotus*, y por *Gonatodes albogularis*, todos de las selvas lluviosas del Caribe. El tipo 2 tambien tiene reproducción durante todo el año con todas las edades representadas en la población durante todo el tiempo, pero el nivel de reproducción y las proporciones de diferentes grupos de edades cambian constantemente con los cambios de estaciones. Este tipo ocurre en climas húmedos que tienen un cambio de estaciones moderado y fué encontrado desarrollado en varios grados en *Ameiva quadrilineata*, *Anolis limifrons*, *Basiliscus vittatus*, y *Leiolopisma cherriei*. El tipo 3 es característico de áreas que tienen una larga estación seca, donde los lagartos confinan su reproducción a las partes más húmedas del año. Al comienzo del período de cría la población consiste esencialmente de adultos en capacidad de reproducirse, pero incrementos subsecuentes de los jóvenes son añadidos hasta que todas las clases desde reciente nacido hasta adolescentes son hallados junto con adultos (entonces disminuidos a pequeños números) al comienzo de cada período de cría. El tipo 3 prevalece en el noreste de Costa Rica y se encuentra en *Anolis cupreus*, *A. intermedius*, *Basiliscus basiliscus*, *Cnemidophorus deppii*, *Gonatodes albogularis*, *Sceloporus variabilis*, y *S. malachiticus*. Esta última especie es una transición con el tipo 4 que de otra forma fué hallado solamente en la iguanida grande, *Ctenosaura similis*. En el tipo 4 hay un período relativamente corto de cría y madurez tardía resultando en una marcada estructura de población que consiste de varios o muchos grupos discretos de edades al menos dos de los cuales son inmaduros. La supervivencia fué estimada de la razón a la cual los individuos marcados desaparecían de las poblaciones en las pequeñas áreas estudiadas, pero parte del reemplazo fué causado por desplazamientos de individuos, y este desplazamiento de espacio no pudo ser evaluado con precisión. En la mayoría de las especies el reemplazo de la población fué rápido, con casi todos los individuos reemplazados en el curso de un año. Fué esencialmente rápido en las especies mas pequeñas de *Anolis*, en *Cnemidophorus deppii*, *Ameiva quadrilineata*, y *Sceloporus variabilis*. En contraste con estas especies la montañosa *Anolis tropidolepis* y las dos especies de basiliscos son notablemente de vida más larga e individuos frecuentemente sobreviven por más de un año. *Ctenosaura similis* está claramente en una clase por sí misma sobreviviendo por mayor tiempo que cualquiera de las especies mas pequeñas de lagartos estudiadas.

Anteriores resultados y predicciones sobre poblaciones de lagartos tropicales son parcialmente anulados por estos resultados. De acuerdo a tendencias indicadas por Tinkle *et al.* (1970) los lagartos tropicales incluidos en este estudio tienen mayormente nidadas pequeñas, y una proporción pequeña de tipos vivíparos a ovíparos comparados con algunos de las zonas templadas. Sin embargo, la falta de correlación entre el tamaño de la hembra y el número de huevos por nidada reportados por Tinkle *et al.* no fué anulado. Se halló que la mayoría de las especies se adhieren a la estrategia de temprana madurez y multiples camadas. Solo una de las 15, *Ctenosaura similis*, se adhiere definitivamente a la estrategia opuesta de tardía madurez y una única camada. Ectimadas por algunos de los criterios fundamentales de selección-*r* y selección-*K* ninguna de las 15 especies puede ser catalogada como una u otra, pero todas fueron intermedias en algún grado, con una mayoría favoreciendo selección-*r*.

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