The Ecology of a Population of *Xantusia vigilis*, the Desert Night Lizard

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INTRODUCTION

Xantusia vigilis was described in 1859 by S. F. Baird on the basis of three specimens sent by John Xantus from Fort Tejon, California. The next specimens were reported 34 years later, when Stejneger (1893) recorded one taken in California and another in Nevada by the Death Valley Expedition of 1891. Shortly thereafter Van Denburgh (1895) discovered that lizards of this species could be found in abundance amid the fallen trunks, branches, and other surface litter that accumulates in stands of Joshua trees (*Yucca brevifolia*) in the western Mohave Desert.

Possibly because *Xantusia vigilis* is available in large numbers and its range is accessible to a number of centers of research, it has become in many ways one of the best known of lizards. Numerous aspects of its biology have been studied: systematics (Klauber, 1931; Savage, 1952, 1963; Tanner, 1957); reproduction (Cowles, 1944; Miller, 1948a, 1954; Heimlich and Heimlich, 1950; Bartholomew, 1950, 1953; Brattstrom, 1951); endocrinology (Miller, 1948b, 1952, 1963); metabolism (Cook, 1949); color change (Atsatt, 1939; Caswell, 1950); behavior (Lowe, 1948; Glaser, 1958); conservation (Cowles, 1952); food habits (Brattstrom, 1952; Wood, 1944b); parasitology (Amrein, 1952a, 1952b, 1953); cra-

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nial morphology (Young, 1942); distribution (Stebbins, 1948a); and thermal relationships (Cowles and Bogert, 1944; Cowles and Burleson, 1945).

Among the authors who have contributed information on the ecology of *Xantusia vigilis,* only Miller presented more than casual notes. In the course of investigating seasonal cycles in testicular and ovarian histology and the correlation of reproduction and growth with seasonal changes in the pituitary gland, Miller (1951) captured several hundred specimens of *Xantusia vigilis.* He made note of their habitat, habits, feeding, reproduction, and growth. In a later paper, Miller (1954) presented additional data on reproduction, particularly as influenced by climatic variation.
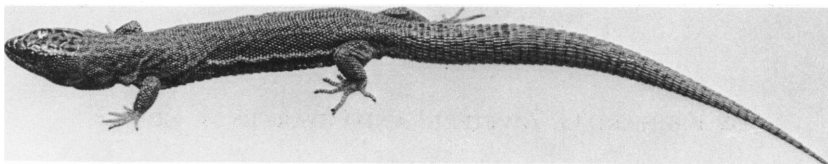

Fig. 1. Adult *Xantusia vigilis;* snout-to-vent length, approximately 41 mm.

The principal object of the present study was to investigate aspects of the ecology of *Xantusia vigilis* that might be illuminated by a long-term program of annual visits to a restricted area. Here we would capture and mark lizards so that individuals might be recognized if they were recaptured. Information on demographic and other aspects of population ecology that could be obtained in this manner would help fill some of the major gaps in our knowledge of the biology of *Xantusia vigilis.*

DESCRIPTION, RELATIONSHIPS, AND DISTRIBUTION
DESCRIPTION

Xantusia vigilis is a small lizard: males reach maturity at a snout-to-vent length of about 36 mm. and a weight of 0.7 gram; females, at 38–39 mm. and about 0.9–1.0 gram (Miller, 1951, p. 119). The maximum snout-to-vent length of males is about 44 mm.; of females, about 50 mm. A complete or perfectly regenerated tail is slightly longer than the snout-to-vent length, so the maximum total length is about 110 mm. The lizard has a relatively elongate, slightly flattened body, with short legs and a thick tail (fig. 1). Granular scales cover the dorsal and lateral surfaces of the body and neck; the venter has rows of enlarged plates. Both original and regenerated portions of the tail bear whorls of enlarged, keeled scales.
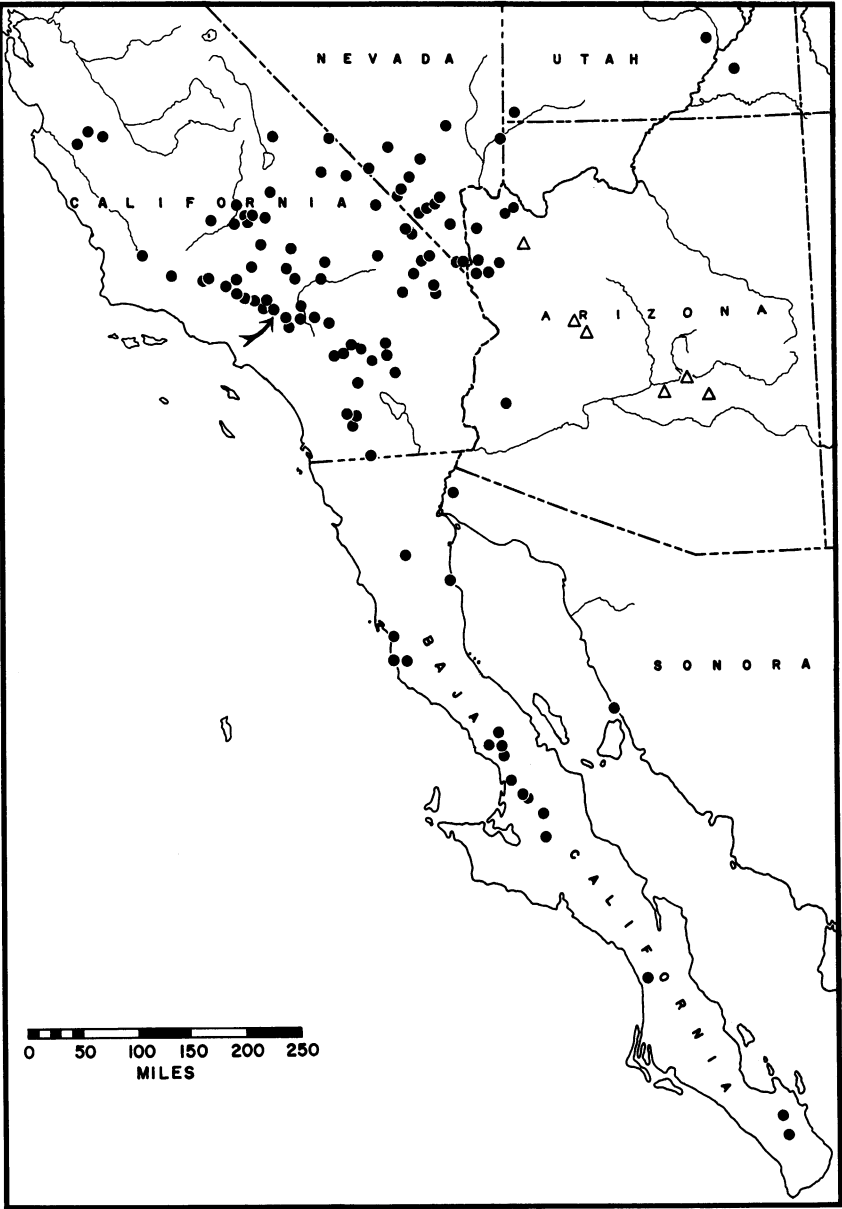
FIG. 2. Distribution of *Xantusia vigilis* (spots) and the closely related species *X. arizonae* (triangles). Arrow points to study area.

RELATIONSHIPS

How many species and genera properly should be recognized in the family Xantusiidae remains unclear. Hecht (1956) admitted three Recent genera, and Savage (1963) suggested a fourth ("Klauberina"): Cricosaura, a monotypic genus known only from a small area in southeastern Cuba; Lepidophyma, with seven "species," ranging from southern Mexico to Panamá; Klauberina, a monotypic genus restricted to three islands off the coast of southern California; and Xantusia, with four "species" (one described since Savage's paper by Webb, 1965) in the southwestern United States and northern Mexico. The widespread and disjunct distribution of the genera suggests an ancient, relict distribution, and the presence in Eocene strata in Wyoming of a form intermediate between Xantusia and Klauberina (Hecht, 1956) supports this view.

DISTRIBUTION

The geographic distribution of Xantusia vigilis and the location of the study area are shown in figure 2. Most of the localities mapped are taken from published sources. Maps published previously (Stebbins, 1948a; Savage, 1963) have indicated that Xantusia is not found in the lower desert regions of California and adjacent Arizona. Savage followed Stebbins' map in general, but incorporated the record of Slevin (1949) for 25 miles south of San Luis, Sonora, as an extension eastward through the delta of the Colorado River. Recent records of X. vigilis in the S. H. (Kofa) Mountains of western Arizona (Lowe, 1964; also A.M.N.H. No. 84318, collected by Willis Gertsch and Vincent Roth) and at Desemboque, Sonora (Malkin, 1962; A.M.N.H. Nos. 73776, 74887, 74888; Felger, 1965), suggest that this species ranges widely throughout the Colorado Desert portion of the Sonoran Desert, but obviously it is neither so abundant there nor so easily collected as in the Mohave Desert.

Four subspecies of Xantusia vigilis are recognized: utahensis in southeastern Utah; wigginsi in the central third of Baja California; gilberti in the Cape region of Baja California; and vigilis throughout the remainder of the range. Xantusia arizonae (indicated in fig. 2 by triangles) is closely similar to vigilis; the two may be conspecific. Another species related to vigilis but widely separated from it geographically has recently been described by Webb (1965).

DESCRIPTION OF THE STUDY AREA

The study area is in Antelope Valley, approximately 5.3 miles east and

1.5 miles south of Llano, Los Angeles County, California, in the south-western corner of the Mohave Desert (fig. 2). The plot lies at an elevation of about 3600 feet on a broad alluvial fan derived from the San Gabriel Mountains which rise abruptly from the desert 1.5 miles south of the plot. The mountains attain an elevation of 7600 feet within less than 10 miles from the study area which lies in their rain shadow.

The area of the plot is approximately 27 acres. It is a rectangle with north and south boundaries 900 feet long and east and west sides 1300
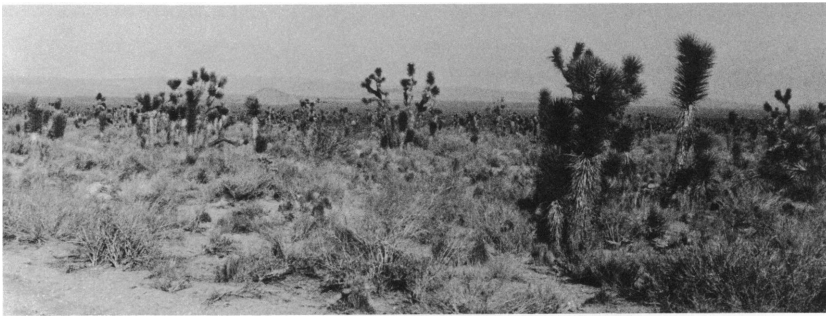

FIG. 3. View of study area. Each clump of Joshua trees that provides suitable shelter (logs or rat nests) is the focus of a local subpopulation.

feet in length. The coarsely sandy ground slopes gently, with a maximum difference in elevation (as estimated from the United States Geological Survey 7.5-minute sheet of the Mescal Creek Quadrangle, 1956) of about 55 feet between north and south boundaries. Minor topographic relief is provided by an ill-defined wash crossing the southwestern quarter of the plot.

The vegetation of the study area is Joshua-tree woodland, as defined by Munz and Keck (1949, p. 103). The physically (but not numerically) dominant species is the Joshua tree (*Yucca brevifolia*), present as scattered individuals and small clusters of trees. The area between and beneath the trees is vegetated by a discontinuous layer of grass (*Stipa speciosa*) and low shrubs (e.g., *Ephedra* sp.), with an occasional larger shrub (*Larrea divericata* and *Lycium andersoni*) or cholla cactus (*Opuntia echinocarpa*) protruding (fig. 3).

Cut off from the coastal region by the San Gabriel Mountains, the study area has an arid, continental climate. A United States Government weather station, Llano Shawnee Hills Ranch, is 1 mile south of the study area at an elevation of 3820 feet. Climatic data for this weather station are undoubtedly applicable to the study area, as the station is only 200
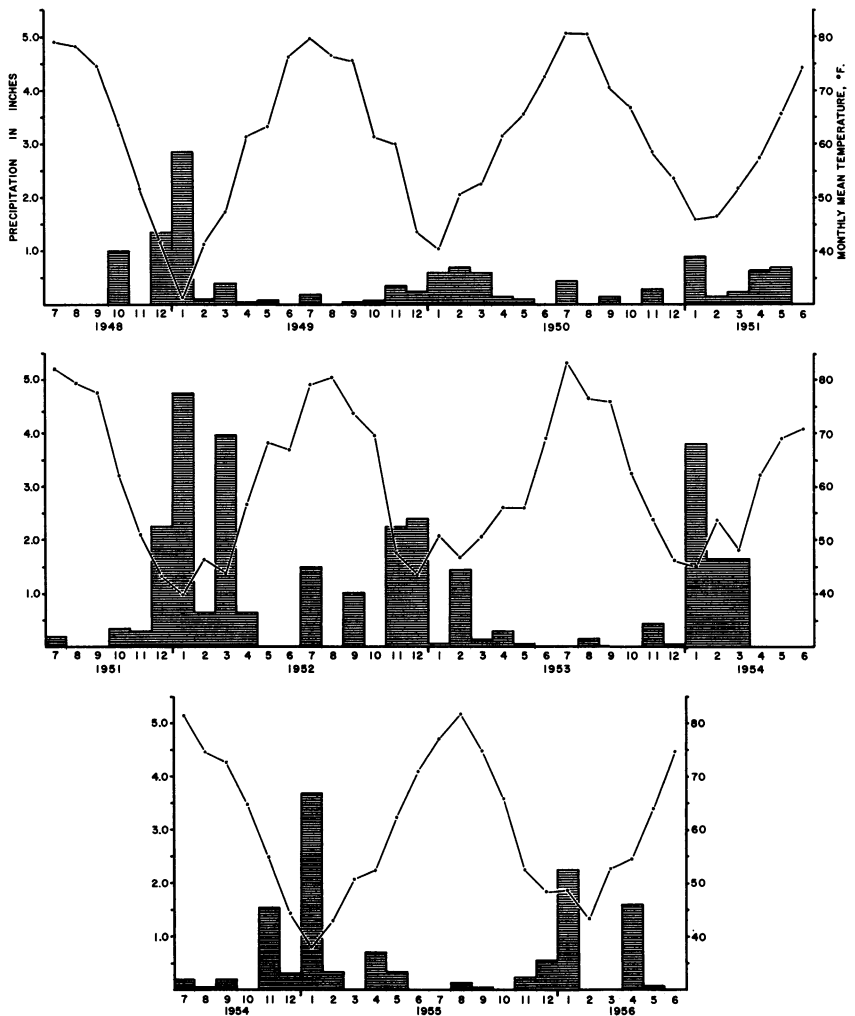
FIG. 4. Climatic data for period pertinent to study: line traces monthly mean temperatures; bars record monthly precipitation.

feet higher than the study area and is in terrain that is similar in topography and vegetation.

The average annual precipitation, largely rain but with some snow in the winter, was 7.61 inches for 41 years of record through 1956. Most of this, 71.2 per cent or a yearly average of 5.42 inches, fell during the winter, from December through March. In some years significant amounts

of rain fall in October, November, or April. Occasional summer thunder-showers add insignificantly to the meager total.

Annual precipitation was slightly subnormal during the seven full years of the study, 1950–1956, averaging 6.90 inches. Wide yearly variation typical of arid regions is seen in the range of total yearly precipitation during this period, 2.61 to 17.17 inches.

Mean monthly temperatures over 38 years ranged from the low in January of 43.1° F. to the high in July of 79.0° F. The yearly range is wide.

FIG. 5. Deteriorated habitat that no longer provides adequate cover. Two lizards were found here in 1949, but none subsequently (photograph taken in 1954).

In the time of our study the lowest and highest temperatures, 17° F. and 107° F., were both attained in 1950. The highest minimum was 23.0° F. in 1953; the lowest maximum, 100° F. in 1952. Monthly temperature and total precipitation for the period pertinent to our study are graphed in figure 4.

The study area is within 4 miles of the edge of the range of the species, for the sharp transition from valley to mountains marks the limits of suitable habitat. It should not be inferred, however, that this marginal location is also marginal in providing suitable habitat. If population density is a reliable criterion, some of the areas most favorable for the species occur along this western edge of the range.

HABITAT

Xantusia vigilis is a secretive animal and seldom seen unless one searches for it. In one or another part of its range it is associated with a variety of kinds of shelter: digger pine logs (Stebbins, 1948a), rocks and boards (Turner, 1959), clumps of low-growing *Yucca* plants of several species (Klauber, 1939; Cowles and Bogert, 1944; Stebbins, 1948a; Tanner, 1957, 1958), dead trunks and fallen stems of giant cacti, *Pachycereus*

FIG. 6. Poor-quality habitat, a log lacking shade or bark but large enough to provide some insulation. One juvenile lizard was found here on the day the photograph was taken.

pringlei (Felger, 1965), and flakes exfoliating from granite boulders (Klauber, 1939). To judge from the number of animals found there, the optimum habitat is provided by the fallen limbs and trunks of Joshua trees (*Yucca brevifolia*). The lizards take shelter between the spikelike, overlapping leaves, within cavities in the dead wood, or on the ground beneath the fallen limbs.

Our study area was in a relatively open stand of Joshua trees (figs. 3, 5, 6). Frequently the most rewarding place to search for *Xantusia* was in nests built by desert wood rats (*Neotoma lepida*) at the bases of Joshua trees or in the midst of clumps of trees (figs. 8, 9). The nest is a jumble of sticks, *Yucca* debris, joints of cholla cactus, stones, and other small objects. A nest

with a rat in residence may be 2 feet in height and 4 feet in diameter. Lizards are found not only in nests deserted by rats but also in those that are still inhabited. On occasion we found lizards within a few inches of inner nest material still warm from the body of the fleeing rat. Inactive nests continue to provide shelter for several years after the rat has left (or died), but decay and compaction of the material of which the nest is constructed eventually reduce its suitability as shelter. In a curious contra-

FIG. 7. Moderately good *Xantusia* habitat. The large log retains much of its insulation-providing bark and leafy covering but is exposed to full sun. Six lizards were found here on the day the photograph was taken.

diction to our experience, Miller (1951, p. 116) found that *Xantusia* was absent from *Neotoma* nests. But Bogert (1930, p. 11), Cowles and Burleson (1945, p. 419), and Wood (1944a, p. 47) mentioned that these lizards are found in wood-rat nests.

The suitability of the shelter provided by fallen logs and limbs of the Joshua tree evidently depends on their size, protection from insolation, and state of decomposition. The log illustrated in figure 5 sheltered two lizards in December, 1949, but we found none there in subsequent years; the photograph was taken in 1954. The absence of bark and leaves greatly reduces the insulating properties of a log, and in this instance the unsuitability is increased by the small diameter of the log and its unshaded situation.

A marginally habitable log is seen in figure 6. It is less rotten than the one shown in figure 5, is of larger diameter, and makes a better and more continuous seal with the ground. One juvenile lizard was found here the day the photograph was taken, and a subadult (not the same lizard) was there the following year.

The log illustrated in figure 7 represents moderately good habitat. The bark and dead leaves add greatly to the insulation and presumably make

FIG. 8. Good habitat provided by the nest of a wood rat (*Neotoma*) at the base of a Joshua tree. Eighteen lizards were found here on the day the photograph was taken and probably at least 26 were present.

up for the complete lack of shade. Six lizards were found here the day the photograph was taken.

The best habitat in our study area is exemplified by the nest of a wood rat shown in figures 8 and 9. We found 18 lizards the day the photograph (shown as fig. 9) was taken and the same number the previous year, when the nest was occupied by a rat. In addition to being partly shaded and well insulated against extremes of heat and cold, the nest presents a formidable barrier to any of the larger predators that might seek entrance (fig. 10).

When faced with severe weather conditions, the vast majority of desert reptiles seek shelter underground in burrows that they or other animals

make. Apparently *Xantusia vigilis* does not do so; hence the importance of adequate surface cover. Miller (1951, p. 115) stated that *X. vigilis* "has never been found to be subterranean in habit, nor does it seek cover in the burrows and retreats of other lizards." The best evidence is that, even during the coldest part of the winter, when the lizards might be expected to go underground, they are abundant in the debris of Joshua trees.

Fifty times during the course of our winter field work we recorded

FIG. 9. The same nest as is shown in figure 8, photographed a year later to show how little the habitat may change from year to year. Eighteen lizards were captured on this occasion, seven of them individuals captured here the previous year.

habitat temperatures intimately associated with the lizards. Temperatures ranged from 0° C. to 17° C., but the vast majority, 82 per cent, were clustered in the range from 6° C. to 12° C. Lizards were found only once each at 0° C., 1° C., 16° C., and 17° C. Temperature gradients within the immediate habitat of the lizard may be extreme. For example, on December 30, 1949, we captured three lizards at 1:50 P.M. when the soil surface temperature beneath the Joshua-tree log was 9.7° C. The air temperature in the shade at an elevation of 2 cm. was 20.2° C., and the surface of the log heated by the sun was 43.0° C. Cowles and Bogert (1944, p. 284) estimated the critical thermal maximum of *Xantusia vigilis* as 38°–39° C. So even in midwinter potentially fatally high temperatures

may be present within a few inches of where the lizards hide. Miller (1951, p. 115) pointed out that in summer the temperature beneath unshaded piles of debris rises as high as to 42° C. and that, as a consequence, during the summer *Xantusia* is almost always under shaded debris.

Suitable habitat in the study area is distributed discontinuously. The map of the collection stations (fig. 11) shows the sites where lizards were collected. Most, but probably not all, suitable sites are indicated on the

FIG. 10. Nest of a wood rat (*Neotoma*). The bayonet-like leaves of the living Joshua tree together with spiny debris such as joints of cholla cactus (*Opuntia*) make the nest virtually impregnable to many potential predators on *Xantusia*.

map. In as much as the study covered a period of seven years, all the sites indicated on the map did not provide suitable habitat at the same time. Many deteriorated through the years, while new ones were added owing to the nest-building activities of wood rats and the falling of dead limbs or trees.

EFFECT OF COLLECTING ON THE HABITAT

Disturbance of the habitat in the course of collecting was inevitable. Wood-rat nests were torn apart, fallen trunks and branches were dislodged, and their dead leaves were pried apart. We tried to strike a balance between disturbance and results, keeping disruption of the habitat
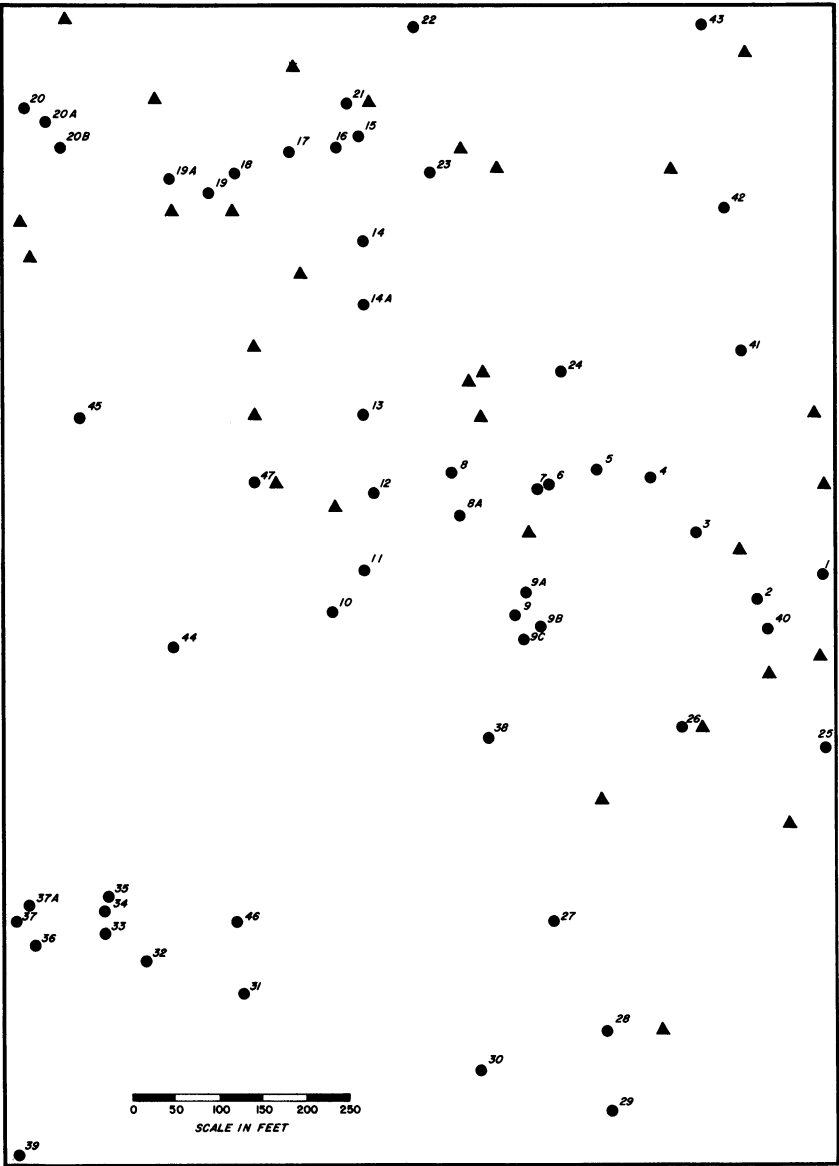
Fig. 11. Distribution of stations in the study area. Numbered spots indicate stations visited every year of the study; triangles, stations investigated only in terminal year.

at as low a level as was compatible with securing an adequate sample of lizards. The lizards are so secretive that even a "scorched earth" policy might not bring all individuals to view. After terminating collecting at a given station, we attempted to return the area to a state as much like its previous condition as possible. In the case of nests actively in use by a wood rat, the rat itself no doubt assisted the process after we were gone.

The repeated capture of individuals at the same station over several years indicates that disruption of the habitat was not too severe. On one occasion we re-examined a station at which lizards had been marked the previous day. Despite a night of freezing rain that left a glaze of ice over the Joshua trees and on the fallen limbs, we found the lizards (plus two that we had missed the first day!) alive and approximately where they had been replaced. Probably the major effect on the habitat of our collecting activity was to hasten natural processes of deterioration that eventually destroy the livability of any site.

METHODS OF FIELD STUDY

On the first day of field study, December 30, 1949, we worked randomly through the area, examining promising sites and capturing the lizards that we found. On capturing a lizard, we marked it by clipping toes and measured its snout-to-vent length to the nearest millimeter. If the tail was broken in the process, we recorded the fact and measured the length of the remaining stub before releasing the lizard where it had been captured. In such a way we handled 133 lizards at 37 sites, or stations, as they are called throughout the rest of this paper. Each station was marked by a numbered (painted) wooden stake.

We returned to the study area for one or two days in December of each year through 1955 (see table 1), visiting each of the original stations every year, measuring and (where necessary) marking the lizards that were captured. When a lizard that had a regenerated tail was found, we noted this fact and recorded the amount of regeneration. New stations were added in 1950 (one), 1952 (seven), and 1953 (two), bringing the total to 47. The temporary wooden stakes used to mark the stations in the first year were supplemented by stakes of iron pipe. A survey made with lensatic compass and steel tape provided the basis for a map of the study area (fig. 11).

The final field work was done in March, 1957, after a lapse of slightly more than 14 months instead of the usual 12. On this occasion Zweifel and Kenneth Norris examined the established stations in the usual fashion and measured (but did not mark) the lizards that were captured. In

addition to working over the old stations, they investigated virtually every other seemingly suitable site for *Xantusia* within the study area.

Mrs. Arlene Lowe, Dr. Kenneth S. Norris, and Dr. William G. Reeder assisted us in the field in one or more years and have our sincere thanks. The senior author participated in all the surveys; the junior author, in all but the last.

Method of Marking Lizards

Lizards were marked by our clipping the toes. Normally, no more than one toe was removed intentionally from a foot, though from some lizards

TABLE 1
Dates of Field Work and Numbers of Lizards Handled

Date	New Lizards	Recaptured Lizards	Total[a]
Dec. 30, 1949	133	—	133
Dec. 30, 1950	47	11	58
Dec. 26, 1951	48	15	63
Dec. 30, 31, 1952	118	14	131
Dec. 30, 1953	146	39	185
Dec. 22, 23, 1954	100	60	160
Dec. 27, 28, 1955	67	42	109
Mar. 3, 4, 1957			
Old Stations	50	31	81
New stations	76	2	78

[a] The totals in this column do not always agree with those in figure 12 because lizards occasionally escaped or were released accidentally before a measurement was made, and figure 12 records only those that were measured.

that had lost a toe or toes before being captured, we clipped another toe from the damaged foot. Rarely, two toes were clipped when one was intended. The minimum number of toes removed from any lizard was two; the maximum, four. In record keeping, we assigned numbers from one to five to the toes of each foot, beginning with the innermost toe on each foot, and identified the feet by appropriate abbreviations. In addition, lizards received consecutive numbers as they were marked. Thus, for example, lizard number 310 is recognized as marked LF (left front)-3, LR (left rear)-2, RR (right rear)-1.

The number of combinations possible by clipping one of five toes on each of four feet greatly exceeds the number of lizards actually marked, and only 38 of the 656 lizards marked had four toes removed by us. Sev-

eral lizards had lost toes from natural causes, however, so that, with the toes removed in our marking, they lacked five or, rarely, six.

SOURCES OF POSSIBLE MISIDENTIFICATION OF MARKED AND RECAPTURED LIZARDS

The greatest source of confusion is natural loss of toes. Such mutilation is not infrequent and probably results mostly from intraspecific fighting such as Lowe (1948) observed in a laboratory population of *Xantusia vigilis* (see p. 27).

Study of the data on lizards handled in one of the sampling periods, March 3–4, 1957, will illustrate the magnitude of the problem and how the difficulties posed by natural loss of toes can largely be circumvented. On these two days we captured 159 lizards. Twelve lizards (7.6%) had lost one or more toes naturally. Seven of the 12 missed toes on only one foot, so obviously were "new" lizards (as all that had been marked by us had at least two toes removed) and were not subject to confusion with lizards that we had marked. Three of the five remaining were recaptured lizards that lacked toes when first marked by us, so were easily identified. The two lizards not eliminated are discussed separately.

If a natural loss of only one toe be assumed the lizard marked LF-2, RF-2+3, LR-2 might be either number 559 or 584, depending on whether RF-2 or RF-3 had been lost naturally. When captured in 1957 at station 25 this lizard measured 40 mm. from snout to vent and had a regenerated tail. Lizard number 559 was marked in December, 1954, at station 25 and at that time was a yearling measuring 29 mm. from snout to vent. Its tail was broken in the capture. Lizard number 584 was marked in the same year at station 44. It was an adult measuring 42 mm. from snout to vent and still had its original tail. Neither lizard was captured during the single intervening collecting period in December, 1955.

Three pieces of evidence make us reasonably certain that the lizard in question is number 559: (1) growth from 29 to 40 mm. in two seasons is only slightly greater than average, and is more reasonable than an apparent shrinkage of 2 mm.; (2) capture of the questionable individual at station 25 is significant, for the lizards are highly sedentary, and number 584 would have to have moved about 750 feet from station 44; (3) number 559 was known to have a broken tail when released in 1954, whereas number 584 had a complete tail, at least when last seen. One of these bits of evidence by itself would not be thoroughly convincing, but the three together point only to lizard number 559.

The last lizard of questionable identity was marked LF-1+5, RR-1. No

lizard marked with toes clipped on only two feet had LF-1 as part of the combination. Therefore the lizard could be only number 56 (originally marked LF-5, RR-1) or a "new" lizard that had lost three toes through natural causes. The almost certain identity of this lizard as number 56, with an additional toe lost from natural causes, is established by the pattern of recapture and growth. It was first marked in December, 1949, at station 17, and at that time was 44 mm. from snout to vent. It was not recaptured until December, 1953, when it was found at station 44 and measured 45 mm. It was recaptured again at station 44 in December, 1954 (snout to vent, 48 mm.), and again at the same station in December, 1955 (snout to vent, 47 mm., the apparent shrinkage being within measuring error). The final capture was in March, 1957, at station 44, and the length was recorded as 50 mm.

By applying the techniques of analysis demonstrated above, or other methods appropriate to a particular situation, we were able to identify the great majority of lizards the identity of which might have been confused by a natural loss of toes. Where any reasonable doubt remained, we discarded the data or have made obvious in the discussion the fact that the data and hence any interpretations are questionable.

Other possible sources of erroneous identification include mistakes in clipping toes or in observing and recording the marks of recaptured individuals. Error of the first sort was readily detected, for, after toes were clipped, the marking formula was read back to the person recording in the field notebook. Any discrepancy was readily noted. Mistakes in observation and recording were not so easily detected but are thought to be insignificantly few.

GROWTH

There are two basic methods that may be used separately or in conjunction for determining the rates of growth of individuals in natural populations. One method involves the collecting of samples over a period of time. Modal size (length or weight) classes may be evident in the samples and may be seen to progress through successive samples, with the growth of the individuals comprising the classes.

If breeding seasons are short and sufficiently separated so that individuals of successive age groups (usually year classes) differ enough in size so that the groups can be distinguished, the method of successive samples may yield accurate results. However, individual variation in growth rate will often be great enough to obscure the boundaries of older age classes and limit the successful application of this method to younger animals

only. Samples collected in several different years and over large geographic areas are particularly liable to erroneous interpretation. For example, Fitch (1954, p. 76) showed that Taylor ("1935" [1936], p. 66) erred in inferring eight or nine annual age groups in *Eumeces fasciatus*, in which only two widely variable age classes actually are recognizable within a single population.

Miller used successive samples (1951, pp. 118–119) in determining the growth of *Xantusia vigilis* through the first three years of life. He collected his samples from a restricted area over a period of one year. He thus avoided the pitfalls of geographic variation and annual variation in growth.

The second method of determining growth rates is to measure, mark, and release individuals, hoping that they may be recaptured and remeasured at a later date. The obvious advantage of this method is that actual amounts of growth are known and are not merely statistical guesses. Variation in rates can more confidently be determined. Disadvantages include a lower order of precision of measurement necessitated by working with living animals, and relatively small numbers of individuals recaptured. Our estimates of growth of *Xantusia vigilis* derive largely from capture-recapture data. Size is expressed as length in millimeters from snout to vent, with accuracy to ± 0.5 mm. Our data show only yearly increments, as field work was carried on (with one exception: March, 1957) only in December. The lack of frequent sampling is of less consequence than might at first be thought, owing to the relatively long life span and slow growth rate of *Xantusia vigilis*.

GROWTH IN THE FIRST YEAR OF LIFE

Miller (1951, p. 118), studying *Xantusia vigilis* collected within about 20 to 30 miles of our study area and in similar habitat, found that the young are usually born in September, though in some years births may take place as late as October. The newborn lizards average 23 mm. from snout to vent, the length ranging from 22 to 24 mm. Evidently little growth takes place in the period of about three months between parturition and late December when most of our samples were measured. In the December samples in which a clearly defined class of young is present (fig. 12: years 1949, 1952, 1954, 1955), the modal size is 22 or 23 mm. The only group of young measured by us in March (fig. 12: 1957) understandably includes larger lizards than the other samples, and has a mode of 24 mm.

The absence of any measurable growth in the first three months of life is not astonishing if habitat conditions are taken into consideration. The liz-
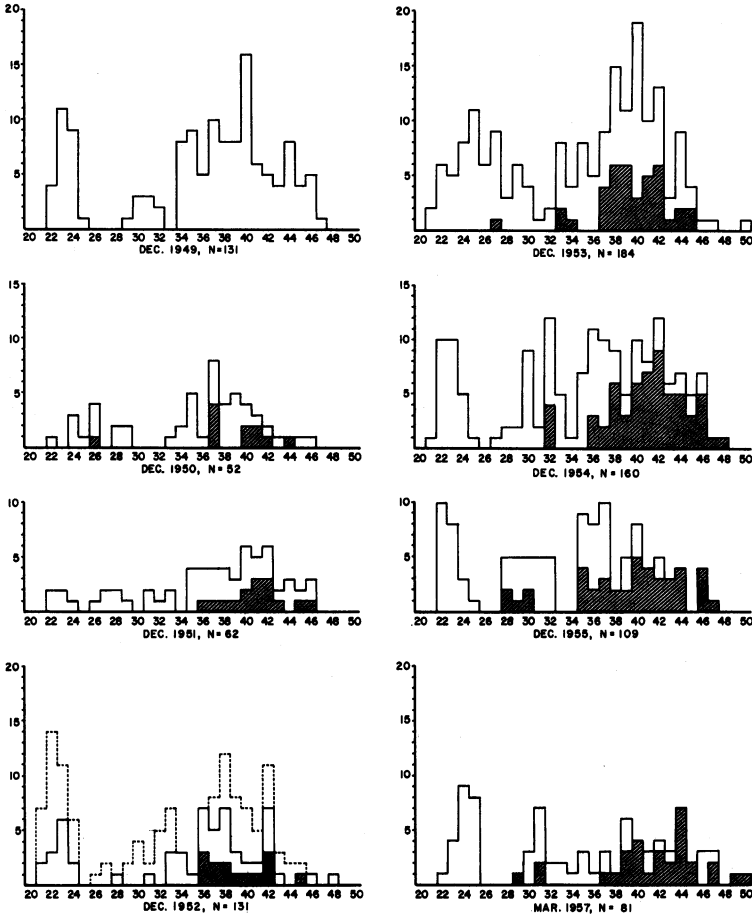
FIG. 12. Composition of yearly samples of *Xantusia vigilis* by size (horizontal axes) and number (vertical axes). Shading indicates marked (recaptured) individuals. Solid lines in 1952 histogram show individuals captured at stations 1 through 38; dotted lines enclose entire sample including lizards from new stations 39–45.

ards are born at a hot, dry time of the year when opportunity for feeding is at a minimum. Presumably they subsist largely on stored yolk, until food becomes more readily available in late winter (February and March), though some feeding undoubtedly takes place during earlier periods of mild winter weather and throughout the autumn.

We marked 139 lizards that, from their size, can confidently be regarded as young-of-the-year. Thirteen of these recaptured a year later had an average length at recapture of 29.6 mm., range 26–32 mm. The

least growth was shown by a lizard (no. 61) that grew from 23 mm. in December, 1949, to only 26 mm. in December, 1950. In 1950 reproductive success was low, presumably because of inadequate nutrition (see p. 40). Another slow-grower (no. 326) measured 22 mm. in December, 1952, and 27 mm. in December, 1953. This year was another in which reproductive success was low.

The size attained appears to be correlated directly with rainfall of winter and early spring, which presumably determines the abundance of food. Though recaptured individuals known to be yearlings ranged in length from 26 mm. to 32 mm., evidently in a particularly poor year even less growth may be registered. For example, the 1952-year class met with unusually dry conditions in the late winter and spring of 1953 when much of the annual growth presumably would take place. Many individuals grew little if at all during this year, so that in December, 1953, the 1952- and 1953-year classes did not show separate modal sizes (fig. 12). Possibly another contributing factor here was the unusually large 1952-year class, with resultant severe competition.

The size-frequency histograms (fig. 12) include two for years in which there is a well-distinguished group of lizards that probably consists of yearlings. These are the 29–32-mm. group in 1949 and the 28–32-mm. group in 1955. In other years the yearling group is less clear-cut: 1950, 1951, and 1953 were years of below-average growth; the 1952 sample shows few yearlings because of poor reproduction in 1951; 1954 has a well-defined yearling peak at 30 mm., but, because of below-average growth the previous year, there is overlap between yearlings and two-year-olds; there is a strong 31-mm. peak in the 1957 sample, but the extra two months of growth over the other samples evidently resulted in overlap with the next year class. Although the number of marked and recaptured young-of-the-year is not large (13), the growth rates determined are consistent with the patterns observed in the size-frequency histograms, and the rates are especially helpful in our interpreting the variation in these histograms.

GROWTH IN THE SECOND YEAR OF LIFE

Data regarding growth in the first year of life make it fairly certain that most individuals measuring 26 to 32 mm. in December are yearlings (approximately 15 months of age), although a few retarded two-year-old lizards likely are included in this range. Years of slow growth (e.g., 1953) add some smaller individuals to the total. We estimate that in the years 1949 through 1955 we handled 136 yearlings, 14 of which we recaptured the following year as two-year-old lizards. These 14 attained an average
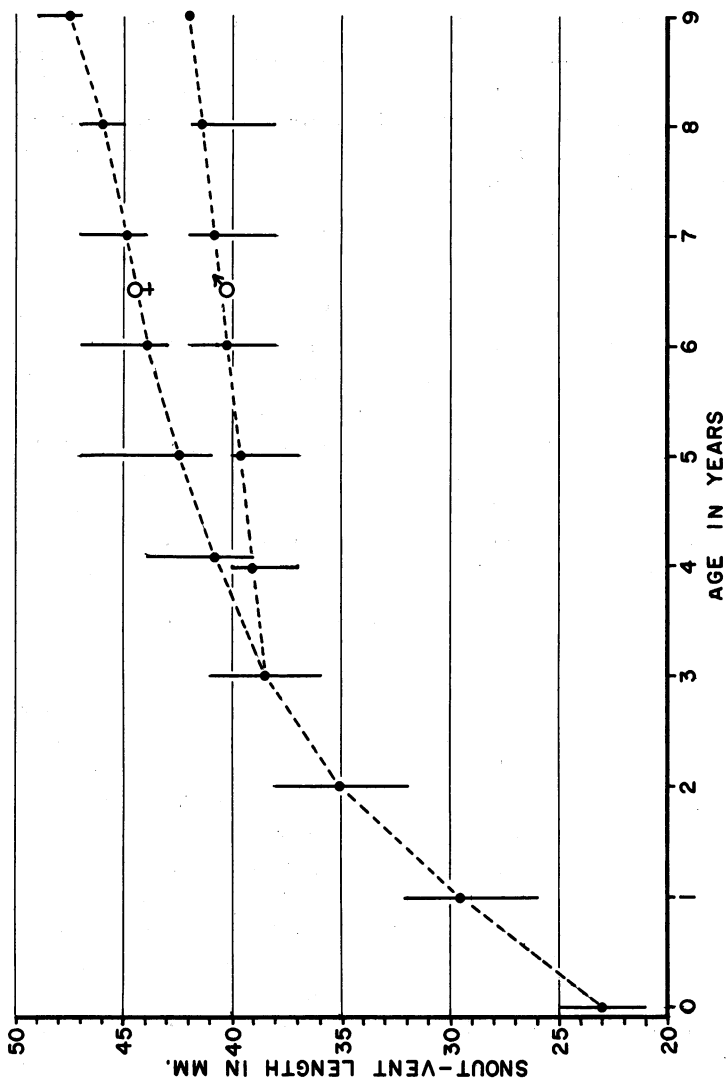
Fig. 13. Growth of *Xantusia vigilis*. Dots mark mean snout-to-vent length of lizards of ages indicated; vertical lines indicate ranges. Broken line merely connects means and does not imply that rate of growth is even throughout the year.

length of 35.1 mm., range 32–38 mm. The individual (no. 391) that measured only 32 mm. as a two-year-old measured 27 mm. as a yearling in 1953. It was one of the brood of 1952 retarded in growth presumably by the poorer conditions prevailing in 1953. Another lizard that suffered similar retardation was number 339, which measured 32 mm. in 1952 and grew to only 33 mm. during 1953.

GROWTH IN THE THIRD YEAR OF LIFE

In the third year of life growth slows markedly, so that there is an overlap in size with lizards of older age groups. As a result, we cannot use all the lizards within the 32–38-mm. range of known two-year-olds as the base for computing growth in the third year, for many of these are older.

Therefore, we restrict our sample of presumed two-year-olds recaptured as three-year-olds to two classes of individuals: lizards previously recorded as young-of-the-year or yearlings and thus of known age, and other individuals that measured 33–35 mm. in one year and were recaptured the following year. Nineteen lizards fit these requirements and at an age of three years averaged 38.4 mm. in length, range 36–41 mm.

GROWTH IN THE FOURTH AND SUBSEQUENT YEARS OF LIFE

According to Miller (1951, p. 119), "females become larger than males and usually average . . . 3 to 4 mm. more in snout-anus length." This situation could come about in one of two ways: individuals of both sexes might grow at the same rate, but the females might live longer and hence get larger, or the growth rates of the sexes might differ. Being unable directly to determine the sex of the lizards in the field, we adopted an indirect method of checking on the relationship of sex to growth.

If, after reaching maturity, males grow at a slower rate than females, the fact should be detectable in records of adult lizards captured two or more times over a period of two or more years. Thirty-eight lizards were recorded enough times as adults to provide usable data. The measurements of these lizards (table 2) fall into two distinct groups. One group that presumably consists of males shows virtual cessation of growth at about 38–42 mm. The size at which growth ceases evidently varies with the individual and may be related to genetic factors or merely to nutrition during the first two or three years of life. The second group includes lizards that did not stop growing at 38–42 mm., but continued on to a size as large as 50 mm. It should be clear that the separation into groups is not arbitrary. The lizards in the first group clearly show plateaus of growth that do not exceed 42 mm., whereas the presumed females show continued steady growth well past that size.

The average rates of growth and sizes plotted in figure 13 for ages four through nine are estimated from the data in table 2. Divergence in growth rates of males and females may begin earlier than is indicated on the graph, but if so the fact could not be detected by our method. Though occasional individuals such as females 398 and 444 (table 2) grow rapidly, the average increment from age four on seems to be about 1.5–2 mm. per year. Males evidently average less than 1 mm. per year after age three, and a few lizards such as numbers 73 and 78 never exceed the average size of three-year-old lizards. No range in size is indicated for nine-year-old males, for all lizards estimated to be this age were of the same length, 42 mm.

COMPARISON WITH PREVIOUSLY PUBLISHED ESTIMATES OF RATE OF GROWTH

Miller (1951, pp. 118–119) gave estimates of the growth rate of *Xantusia vigilis* in the first three years of life based on measurements of lizards captured from August, 1940, to August, 1941, in a region close, and similar ecologically, to our study area. He stated that one-year-old animals average 29 mm. in snout-to-anus length; two-year-old lizards average 36 mm.; and three-year-old lizards average 38–39 mm. Miller also provided a graph on which the average snout-to-vent length at intervals throughout the first three years of life was plotted. The average size corresponding to our December yearlings is 31 mm.; to our December two-year-olds, 37 mm.

The average sizes given by Miller are slightly greater than we determine for lizards of the same age, though within our range of variation: 29.6 versus 31 mm., and 35.1 versus 37 mm. This difference might result from differences in precision of measurement, with Miller's measurements of dead animals being more accurate. Another possibility is that Miller's sample was taken at a time when environmental conditions promoted better than average growth. Rate of growth and reproductive success seem to be correlated directly with rainfall. During the period of November, 1940, through April, 1941, the season pertinent to Miller's study, 14.64 inches of rain fell at the Llano station near our study area. This figure is more than 16 per cent greater than was recorded in any season during our study. During the same period, 27.80 inches were recorded at Fairmont and 17.52 inches at Palmdale, two collecting localities mentioned by Miller. Thus Miller's data were collected in an exceptionally wet period in places where rainfall also normally exceeds that of our study area. Probably his data reflect an abnormally high rate of growth, though the average rate of growth in his study areas in the first two

TABLE 2

FIELD NUMBERS (IN PARENTHESES) AND SNOUT-TO-VENT LENGTHS OF INDIVIDUALS OF
Xantusia vigilis CAPTURED IN SUCCEEDING YEARS[a]; ACCURACY TO ± 0.5 MM.

Presumed Males	Presumed Females
(9) 42—42—43—42	(23) 42—42—45
(18) 37—37—38—39	(32) 44—X—45
(33) 40—X—41	(56) 45—48—47—50
(43) 42—X—X—X—41	(144) 46—46—45
(68) 37—37—38—39	(182) 46—X—X—47
(73) 38—X—X—X—X—38	(208) 38—X—43—46
(78) 38—X—38	(214) 44—X—X—46
(80) 40—40—40—39—41	(275) 44—X—46
(89) 42—X—X—42	(290) 42—X—45
(93) 36—37—X—36—38	(312) 42—42—46—46—47
(131) 40—X—X—X—42	(322) 39—40—43—44—45
(149) 42—42—X—42	(334) 38—39—43
(376) 40—X—X—40	(362) 40—41—X—44
(381) 40—41—41	(366) 38—X—X—43
(434) 42—X—42	(398) 30—35—39—44
(466) 40—X—39—40	(411) 35—X—X—44
	(423) 41—X—44
	(442) 44—45—46
	(444) 33—41—43—47
	(464) 41—X—44
	(467) 44—46—46—49
	(525) 40—X—44

[a] An X indicates a year in which the lizard was not captured.

years of life may nevertheless normally be greater than in the population we sampled.

The estimate of average size at three years derived from our data and that given by Miller are closely similar: 38.4 mm. and 38–39 mm. This agreement is not inconsistent with what has been written in the preceding paragraph concerning growth in the first two years, if we assume that a marked slowing of growth takes place as a length of 38–39 mm. is attained. The lizards of the population in our study area or any other are, in effect, given time to catch up.

The maximum snout-to-vent length of *Xantusia vigilis* evidently is about 51 mm. Fisher (1936, p. 174) recorded 50.9 mm. as the maximum in a series of 106 lizards, and 50 mm. is the maximum size recorded in the cruder measurements (to the nearest 1.0 mm.) of our field work. Judged from our data, males longer than 42 mm. in the population we studied

Size Class: Snout-to-Vent Length in Mm.	Number of Lizards in Class	Number with Tails Regenerated	Percentage of Lizards with Tails Regenerated
21–24	47	4	8.5
25–32	71	22	31.0
33–36	49	23	46.9
37–50	177	126	71.2
Mean	—	—	50.9

[a] Well-regenerated tails could not be distinguished externally from original tails; hence, the true number of lizards that lost their tails is higher than is tabulated here.

would be quite exceptional. Turner (1959) recorded a length of 44 mm. for a male from the Panamint Mountains, Inyo County, California.

LOSS AND REGENERATION OF THE TAIL

In common with many other lizards, *Xantusia vigilis* can break off part of the tail and later regenerate the lost member. Discussions of tail regeneration in lizards commonly include statements to the effect that a regenerated tail may be distinguished from an original one by differences in color and scutellation, and that a regenerated tail never attains the size of the lost portion it replaces (or the size the original tail would have reached if the lizard was young and still growing). Such is clearly not the case in *Xantusia vigilis*, for tail regeneration can be virtually perfect, at least so far as color, scutellation, and size are concerned.

The possibility that we might not be able to distinguish regenerated from original tails first came to our attention when we found that recap-
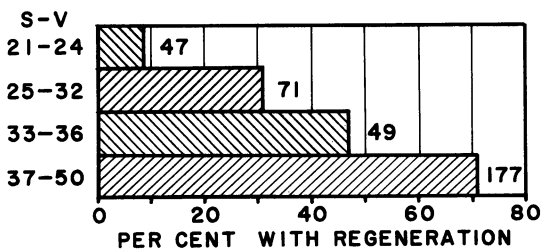

FIG. 14. Percentages of *Xantusia vigilis* in four size groups, showing obvious tail regeneration; numbers at ends of bars give sizes of samples.

tured lizards that had apparently complete, original tails had been re-
corded in earlier years as having regenerated tails. Confirmatory data
came from an experiment in the laboratory. In determining the amount
of weight lost with an autotomized tail (discussed in a following section),
we caused 17 lizards to drop their tails. The tails were classified as orig-
inal or regenerated under examination with the aid of a binocular dissect-
ing microscope. The autotomized tails were then X-rayed, and we found
that no fewer than four of eight that had appeared to be original actually
were regenerated. The presence of a continuous cartilaginous rod in place
of the vertebrae of the original tail is evident under X-ray.

Although we lack extensive data on relative tail length in *Xantusia
vigilis,* we have enough information to indicate that a regenerated tail of
an individual may be as long as or even longer than an original tail of an-
other lizard of about the same size. For example, among four lizards from
40.0 to 42.5 mm. in snout-to-vent length, the relatively longest tail, 57.7
per cent of the total length, was original. The next longest, 56.5 per cent,
was about 26 per cent regenerated. The third was an original tail 55.6 per
cent of the total length; the fourth, a regenerated tail 55.3 per cent of the
total length, with 51 per cent of the tail regenerated.

In the course of our field work we noted the condition of the tail of each
lizard captured. It is now evident that many of those classified as having
complete, original tails must have had regenerated tails, but the data
gathered are useful in indicating a minimum figure for the incidence of
the loss of tails. Data for the years 1953 and 1954 are presented in table
3 and figure 14. Loss and regeneration of the tail is evidently a common
experience, for more than 70 per cent of the lizards of adult size obviously
have lost part of the tail at least once, and undoubtedly additional regen-
erated tails went undetected by us.

Autotomy is commonly thought of in terms of survival value in that it
enables a lizard to escape a predator. With this in mind, it might seem
that lizards in the population we studied were exposed to high predation
pressure if so many of the lizards had been forced to the last resort of au-
totomy in order to survive. This interpretation, however, does not agree
well with features of the ecology of *Xantusia* First, there are relatively few
potential predators in the immediate habitat of the lizard, and none of
these is at all abundant. Second, the exceptionally low reproductive po-
tential of *Xantusia,* the high population densities present, and the "top-
heavy" age structure, with a relatively large number of adult individuals,
all suggest that population turnover is slow and, hence, that predation is
not severe.

For a comparison we may turn to the data on *Sceloporus olivaceus* given

by Blair (1960, pp. 48–49). Although beset by a number of predators and undoubtedly more exposed to predation than the secretive *Xantusia,* only about 35 per cent of the female *Sceloporus* and 50 per cent of the males had lost the tail by an age of three years. In terms of average life span, a three-year-old *Sceloporus* is equivalent to a *Xantusia* eight or more years of age, and by this age virtually all individuals of *Xantusia* have lost the tail at least once.

Undoubtedly predation accounts for some instances of autotomy in *Xantusia,* but we suspect that intraspecific fighting, in which toes (and even lower extremities) as well as tails are lost, is responsible for most of it. Lowe (1948) observed fighting that involved actual biting, not just bluffing, among both male and female *X. vigilis* in a laboratory colony, and lizards kept by the senior author lost toes and tails, evidently as a result of attacks by their cage mates. Heimlich and Heimlich (1947) and Brattstrom (1952) reported instances in which some individuals of *Xantusia* ate the tail of another. The first reported instance occurred in captivity, and Brattstrom could not say whether the three he reported had occurred among captive or wild animals. That Brattstrom (*ibid.*) found tails in only three of almost 300 stomachs that he examined does not necessarily mean that autotomy occurs only rarely in fighting; it is likely that only a few of the tails lost are eaten.

Studies of other lizards, such as *Sceloporus* (Blair, 1960), *Eumeces* (Fitch, 1954), and *Leiolopisma* (Barwick, 1959), show that important factors influencing the rate and amount of regeneration following loss of the tail include the size (or age) of the lizard, season of the year (and, hence, activity of the lizard), and the point on the tail at which breakage occurs. In general, a young lizard losing the tail relatively close to the base will exhibit more regeneration than an old lizard losing a smaller portion of the tail. Presumably the same factors influence *Xantusia,* but our data are too few and too incomplete to permit detailed analysis of the sort undertaken by the authors cited above. Inasmuch as we could hope to recapture lizards only after a minimum lapse of one year, we did not deem it practical to attempt to determine rates and amounts of regeneration in the field. Even when the exact date of loss of a tail is known (as for example, loss in capture) and the lizard was recaptured the next year, there was no way of being certain that one or more subsequent losses and regenerations had not taken place during the year.

Some data are at hand on the rate of regeneration in a small laboratory population. Fourteen lizards that had lost from 65 per cent to 87 per cent of the length of their tails replaced from 37 per cent to 66 per cent (mean, 53.1 per cent) of the amount lost in 105 days. The mean rate of regenera-

tion was 0.18 mm. per day, range 0.15–0.22 mm. It is likely that the averages and lower limits observed were influenced by interference with regeneration due to fighting.

WEIGHT LOSS IN AUTOTOMY

The tail of *Xantusia* probably serves as an organ for the storage of fat, as it presumably does in other lizards. It is of interest to determine how
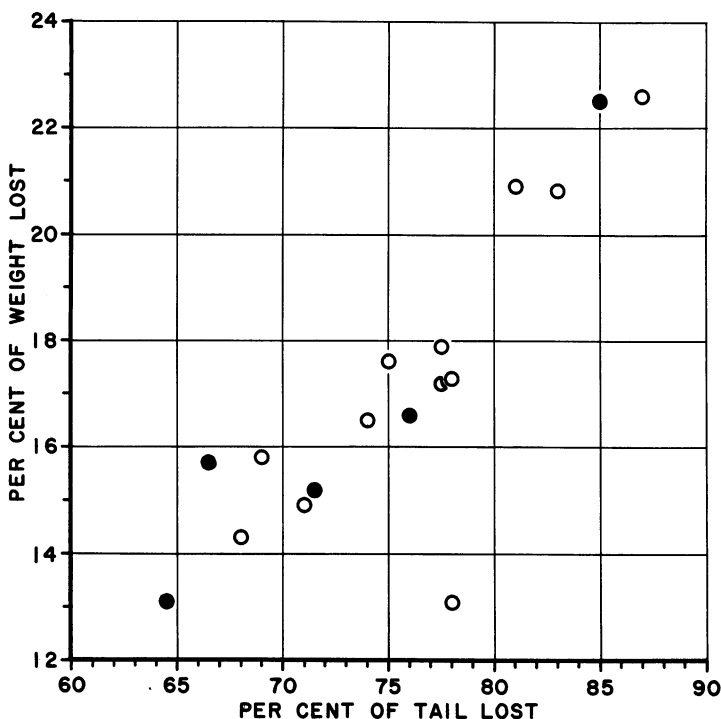
FIG. 15. Relationship of amount of tail (percentage of tail length) lost in autotomy to amount of body weight lost in *Xantusia vigilis*. Dots indicate original tails; circles, regenerated tails.

much weight (and thus, to some extent, how much stored energy) the lizard loses with the tail.

Seventeen lizards were weighed, made to lose the tail, and reweighed. The data resulting from this experiment are presented in figure 15. The amount of weight lost is, of course, dependent on how much of the tail was dropped. The relationship of the percentage of the tail lost to the per-

centage of the total weight lost is curvilinear, because the loss of a greater amount of tail means that more of the relatively thicker proximal part is given up. Lizards in this experiment lost from 13.1 to 22.6 per cent of their total weight. The data are biased to the extent that we have no measurements of weight loss associated with the loss of small amounts of tail. There is no clear distinction in weight between original tails and well-regenerated tails. The only spot on the graph conspicuously out of line represents a tail, the lost portion of which was wholly regenerated, that was well short of complete regeneration.

INFLUENCE OF AUTOTOMY ON GROWTH OF THE BODY

The tail comprises a sizable amount of the bulk of an individual of *Xantusia*, and it is reasonable to suppose that one devoting energy to regenerating the tail might do so at the expense of the growth of the body as a whole. Data to substantiate this supposition should come from young, presumably rapidly growing individuals. We have records of three lizards that bear on this question.

Lizard number 580 measured 23 mm. and had a complete tail when marked in December, 1954. When the lizard was captured one year later, its body length was 28 mm., and there were 23 mm. of regenerated tail on a 5-mm. stub. Yearling lizards in 1955 ranged in length from 28 to 32 mm., mean length 30 mm. (fig. 12), so this individual was at the lower limit of growth for its year class.

Lizard number 391 measured 27 mm. when captured in December, 1953. The tail was broken in capture. One year later the lizard had 33 mm. of regenerated tail and had attained a body length of 32 mm. A yearling body size of 27 mm. and a size of 32 mm. at two years of age are both well below average.

Lizard number 339 measured 32 mm. when it was captured and its tail broken in December, 1953. One year later the lizard measured only 33 mm. and had 20 mm. of regenerated tail. The amount of body growth recorded is decidedly below average.

In all three instances the lizards showed less than average growth. Although this evidence is suggestive, it is hardly conclusive. Lizard number 391, for example, was of below-average size when it lost its tail, and the relatively small size it attained the following year might merely reflect its "runt" condition. Undoubtedly many factors contribute to the amount of growth a lizard attains in a given year, and loss of the tail might be a decisive factor only when other conditions were marginal, for example, when food was in unusually short supply.

MOVEMENTS

Habitat favorable to the lizards is distributed discontinuously over the study area. Our studies of movement concern dispersal from one station to another, not movement within one station (see fig. 11). Thus, we are not concerned with purely local shifts such as occur, for example, when a lizard is found under one end of a log of a Joshua tree one year and the following year 10 feet away under the other end of the same log or beneath a closely adjacent one. However, from our experience elsewhere with *Xantusia* during the spring and summer months, we suspect that a study carried on during a season when the lizards are more active, particularly during the breeding season, would reveal non-random distribution within a given station. As Miller (1951, p. 115) noted, "during the spring, summer, and early fall, seldom more than two or three individuals are found within the limits of an isolated branch or in a small pile of debris . . . . it seems likely that the phenomenon of spring and summer isolation is related to a condition of territoriality." Lowe (1948) recorded fighting among captive *Xantusia* and inferred that this is related to territoriality.

In the course of our study we marked 656 lizards and recaptured 152 of them a total of 216 times. In only 19 instances was there an apparent change of station; the remaining 197 recaptures (91%) took place at the same station at which the respective lizards were found from one to six years before, as follows:

> 98 one year later
> 60 two years later
> 27 three years later
> 8 four years later
> 3 five years later
> 1 six years later

In many instances a lizard was taken at the same station in successive years, whereas in other records there are gaps between recaptures (table 2), but there is little reason to think that a lizard left and returned in a later year. With regard to these gaps, it is more likely that the lizard was present but not captured.

The minimum (straight-line) distances traveled by the lizards recorded at stations other than those at which they were first found ranged from 36 to 1050 feet, with a mean of 353 feet. (The two most remote stations were 1500 feet apart.) Six of the 19 recaptures with movement occurred after a lapse of just one year. These movements ranged from 36 to 430 feet, mean 140 feet. The greatest distance moved, 1050 feet, involved a period of three years; and the next greatest, 1000 feet, five years.

The sample of 19 lizards that traveled is too small to permit a firm conclusion, but there is no evidence that lizards of any given age (or size) group are more likely to move than are those of another group. Five lizards that traveled were young-of-the-year when last recorded previous to moving, three were yearlings, and 11 were two years or more in age. The proportion is not dissimilar to the general age distribution in the population during an average year. In many instances two or more years went by before the lizard was recaptured, so its age at moving cannot closely be estimated.

The picture that emerges from these data is one of a highly sedentary population. Even the few movements recorded may be excessive, as there is reason to suspect that some of the lizards that were thought to have moved actually may be individuals that lost toes naturally, so were confused with marked lizards. Ten of the 19 that apparently moved lacked only two toes. This number is far out of proportion to the total number of lizards marked with only two toes removed. Lizards marked by the removal of two toes constitute 18 per cent of the total of 656 that were marked, but represent 53 per cent of those that apparently changed station. However, in only one instance can we point out a case almost certainly involving two individuals with the same toes missing. Lizard number 23, a young-of-the-year with a snout to vent length of 24 mm., was marked at station 8 in 1949. In 1952 we captured, 425 feet away at station 42, a lizard that measured 42 mm. and had the same two toes missing. The average length of three-year-old lizards is 38.4 mm., and the maximum otherwise recorded is 41 mm. Moreover, the intervening years, 1950 and 1951, were notable for the poor reproduction and poor growth experienced by *Xantusia*. It is quite unlikely indeed that this lizard was a recaptured one that had both moved and exhibited exceptionally vigorous growth. Lizards marked as young-of-the-year are much less likely to be recaptured than are lizards marked as adults, which further increases the already high probability that two individuals were involved.

About 77 per cent of the lizards marked never were recaptured. Of course, many of these merely eluded capture in subsequent years, and many others died before recapture was possible, but we must consider the possibility that emigration was responsible for a significant portion of the apparent loss. The capture every year of unmarked adult lizards might indicate that a considerable passage of individuals into and out of the study area took place.

If much movement of this kind takes place, it is reasonable to expect much more evidence for it among the recaptured lizards. A generous estimate of 9 per cent of changes of station is not evidence of a highly vagile
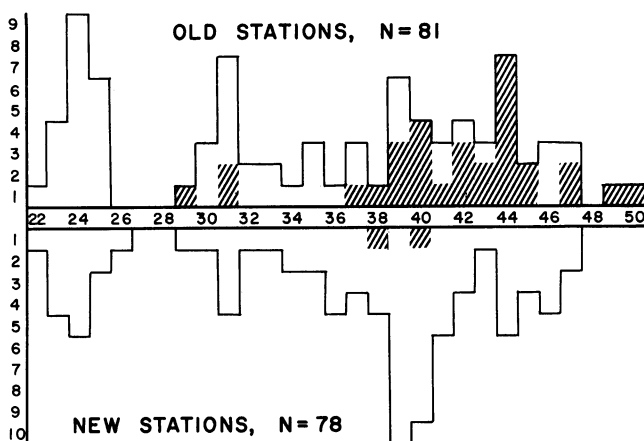
Fig. 16. Comparison of numbers and sizes (by snout-to-vent length) of individuals captured in March, 1957, at stations regularly visited in previous years ("old") and stations within the study area examined for the first time. Shading indicates recaptured individuals.

population. Other evidence strongly supports the view that movement is not extensive. The last time the population was sampled (March, 1957) the senior author and Kenneth S. Norris not only collected at all the stations regularly visited during the study but also investigated every other promising site within the study area. At the old stations 61 lizards of yearling size and larger (lizards that had been exposed to capture in one or more previous years) were captured; 31 of these (50.8%) were marked. At the sites undisturbed in earlier years 65 lizards of yearling to adult size were found, of which only two (3.1%) were missing two or more toes (fig. 16). The spatial relationships of the stations visited regularly and those visited only at the terminal date are shown in figure 11. It is evident that there is a minimum of passage of individuals between sites even reasonably close together, so it is unlikely that emigration or immigration plays a large or important part in determining the population structure.

Probably an important stimulus to movement is the gradual deterioration of the habitat at a given site. The lizards are long-lived, and many may outlive the advantageous habitability of a deserted rat nest or the decaying log of a Joshua tree. In at least five of the instances of movement that were recorded, the site abandoned proved in subsequent years to be devoid of lizards or offered, at the best, decidedly suboptimal habitat. In other cases lizards left well-populated sites, possibly in response to population pressure.

POPULATION STRUCTURE

METHODS

The basic data of population structure are the number, age, and sex of individuals comprising the population. Because we were unable to determine the sex of living individuals of *Xantusia* in the field, this datum is not available. When it is necessary to take sex into consideration we assume that a 1/1 ratio exists.

We estimated the age structure of each yearly sample in the following way: Using the growth curve (fig. 13) as a guide, we assigned each lizard an estimated age based on the youngest age at which it could have attained the observed size. Thus, for example, a lizard 37 mm. in length would be assumed to be two years old, though it might actually have been older.

There were exceptions to this policy of determining age. When one or more of the years of poor growth were involved (1950, 1951, 1953), we took the fact into consideration and modified the estimated age accordingly. For example, a lizard measuring 41 mm. might have been an exceptionally rapidly growing three-year-old, but if one of the poor years was included in its growth period it was more realistic to assign an age of four years to the lizard. In many instances lizards were recaptured two or more times. With two or more measurements of one individual, it often was possible to make a more accurate estimate of its position in the size-age curve.

Determining the number of young-of-the-year in most samples presented no problem: Individuals of the 21–25-mm. group in size obviously belong to this class (fig. 12). The year 1953 presented special difficulty, for in this sample there was no clearly defined group of young lizards. Comparison with the data of other years and the knowledge that a marked lizard that measured 27 mm. in 1953 was 22 mm. long in 1952 (and, hence, was of the 1952 brood) make us certain that the 21–31-mm. range in size in 1953 included two age classes: young-of-the-year and yearlings. It was necessary to be even more arbitrary than usual in assigning ages to the lizards in this mixed group. We assumed that individuals measuring 21–23 mm. were young-of-the-year. We know that in other samples lizards of this age measuring 25 mm. are rare, and even lizards 24 mm. in length are less abundant than those of smaller size (fig. 12). Comparison with other samples suggests that it would be reasonable to consider four individuals measuring 24 mm. and one measuring 25 mm. as young-of-the-year, regarding the balance of those 24–31 mm. long as yearlings.
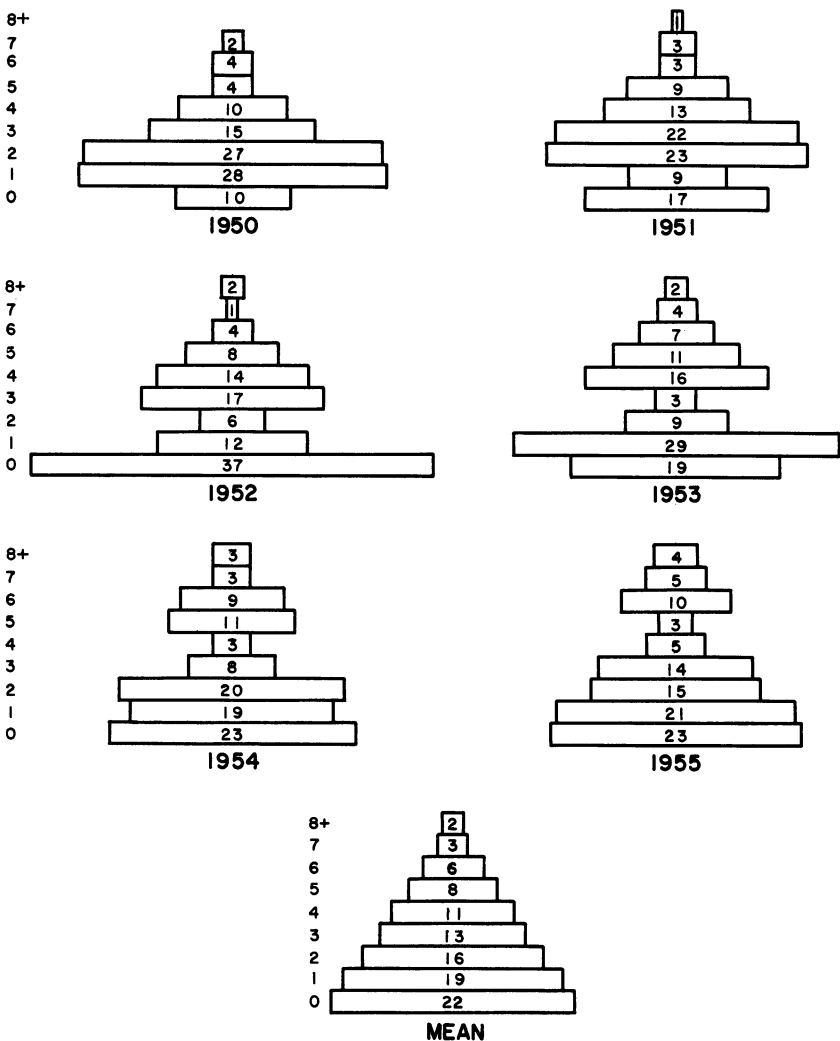
FIG. 17. Estimated composition of population by age in years and per cent for six years, based on sampling in December.

These procedures provided an estimate of the age structure of the yearly samples. It was evident, however, that the various age classes were not represented in the samples in the same proportions that they existed in nature. As figure 12 shows, many yearlings were captured, but relatively few of these had been marked the previous year. This fact suggests

TABLE 4

ESTIMATE OF NUMBERS AND AGES OF *Xantusia vigilis* PRESENT AT STATIONS REGULARLY STUDIED IN DECEMBER OF 1950 THROUGH 1955; PERCENTAGES GIVEN IN PARENTHESES

Year	Age in Years									Total	Adult Females
	0	1	2	3	4	5	6	7	8+		
1950	27 (10.5)	72 (27.9)	70 (27.1)	38 (14.7)	26 (10.1)	10 (3.9)	10 (3.9)	5 (1.9)	0 (0.0)	258	45
1951	44 (16.6)	25 (9.4)	62 (23.4)	58 (21.9)	34 (12.8)	23 (8.7)	8 (3.0)	8 (3.0)	3 (1.1)	265	67
1952	125 (36.8)	39 (11.5)	21 (6.2)	57 (16.8)	47 (13.8)	29 (8.5)	13 (3.8)	2 (0.6)	7 (2.1)	340	78
1953	57 (18.8)	89 (29.4)	28 (9.2)	10 (3.3)	49 (16.2)	32 (10.6)	21 (6.9)	11 (3.6)	6 (2.0)	303	65
1954	54 (22.8)	44 (18.6)	48 (20.2)	19 (8.0)	7 (3.0)	27 (11.4)	22 (9.3)	8 (3.4)	8 (3.4)	237	46
1955	34 (22.5)	32 (21.2)	23 (15.2)	21 (13.9)	8 (5.3)	4 (2.7)	15 (9.9)	8 (5.3)	6 (4.0)	151	31
Means	57 (22.0)	50 (19.3)	42 (16.2)	34 (13.1)	29 (11.2)	21 (8.1)	14 (5.4)	7 (2.7)	5 (1.9)	259	55

that young lizards were less likely to be captured than older ones, thus were under-represented. In order to get as complete a picture of the population as possible, we used the procedure described in the following paragraph.

For each collecting station we constructed a table with a vertical column for each year of the study and entered the field number, size, and estimated age of each lizard captured at the station in each year. In instances in which a lizard was recaptured after a lapse of one or more years, its presumed presence in the population (and age) was entered in the intervening years.

We are aware of a number of inaccuracies in the method. There must have been many lizards present that never were captured. Probably more of the young and the yearlings, both of which are difficult to find, than adults were in this group. Another source of error lies in our lack of knowledge of the fate of lizards after their last capture by us. Many of these must have lived for one or more years after capture, but for our purposes they must be treated as having died (or otherwise left the population) immediately after the last capture. Inaccurate estimates of the ages of lizards would influence the calculations of numbers of lizards thought to be present in the years preceding those in which the lizards concerned were first captured.

The possibility that migration was a source of error deserves mention. Though we assume that a lizard (other than one of the class of the current year) was present in the population for one or more years prior to its first capture, we cannot know definitely that it did not just migrate into the area. However, the evidence from marked and recaptured animals (see pp. 30–32) indicates that *Xantusia vigilis* is extremely sedentary; we doubt that migration is a significant source of error.

Any estimates of population size and age distribution are only rough approximations of the true situation. Most of the sources of error in our estimates are conservative. The number of lizards is undoubtedly underestimated. The average age of the lizards captured is very likely greater than is estimated, but such possible error is offset by the higher proportion of young lizards that eluded capture.

Numbers and Age Distribution

The estimated numbers and ages of lizards present at the stations regularly visited in midwinter of the years 1950–1955 are given in table 4. No estimate is given for 1949 because the bias against accurate estimate of the ages of older animals is too strong, when there are no data from one or more previous years. The terminal year of the study, 1956, is likewise

omitted, because the method of estimation used depends to a large extent on capturing in later years individuals that were present but unrecorded in the year in question. Indeed, the very low estimated size of the population for 1955 probably reflects this factor.

The most remarkable feature of the population that these data bring out is the high proportion of mature individuals present. If a 1/1 sex ratio is assumed, as well as that half of the individuals two years old are mature (males mature at two years, females at three: Miller, 1951), an average of 51 per cent of the winter population consists of mature lizards. Also brought out by the data is the prolonged effect on age structure of the two years of poor reproductive success (1950 and 1951). This shows in the "pinched" appearance of the polygons (fig. 17). Because of the long life span of these lizards and the normally low turnover, however, the occurrence of two consecutive years with relatively low reproductive success produced no serious effect on the population.

The average age structure of the population is represented by a symmetrical pyramid (fig. 17). Probably our methods of estimating ages and numbers err most greatly in our underestimating the number of juveniles and in our underestimating the ages of the larger lizards, so the pyramid probably should have a wider base and narrower, higher apex. In considering the age distribution pictured, the reader should not confuse "average" with "normal." In order for a natural population to have this average distribution of ages, the population would have to experience eight or more consecutive years of average reproductive success. Because reproductive success is correlated closely with rainfall during the winter, and because rainfall varies so much from year to year, there is little likelihood that such an average age structure ever exists in nature—at least for very long.

POPULATION DENSITY

The number of lizards estimated to be present at the stations regularly visited in our yearly surveys ranges from 151 to 340. However, as noted above, these surveys did not include all the suitable habitat within the study area. In the terminal survey, when all suitable habitat was investigated, approximately equal numbers of lizards were found in the stations visited yearly and in sites that previously had been undisturbed (fig. 16). Thus it is reasonable to suppose that the total population of the study area was about double that present at the stations studied. The estimates and expressions on an acreage and square-mile basis are presented in table 5.

The only published estimate of population density in *Xantusia vigilis* is

TABLE 5

ESTIMATED POPULATION DENSITY OF *Xantusia vigilis* IN DECEMBER;
ESTIMATED NUMBER OF ADULT FEMALES GIVEN IN PARENTHESES

Year	Number of Lizards Counted	Estimated Number at Stations Regularly Studied	Estimated Corrected for Unstudied Habitat	Lizards per Acre	Lizards per Square Mile
1950	58	258 (45)	516 (90)	19	12,160
1951	63	265 (67)	530 (134)	20	12,800
1952	132	340 (78)	680 (156)	25	16,000
1953	185	303 (65)	606 (130)	22	14,080
1954	160	237 (46)	474 (92)	18	11,520
1955	109	151 (31)	302 (62)	11	7,040
Means	118	259 (55)	518 (110)	19	12,267

that of Miller (1951, p. 116), who estimated "approximately 2,000 indi-
viduals per square mile." He also suggested that, in especially favorable
sections, the population might be two to three times this figure. Our data
suggest much greater density, on the order of five or more times as great,
with an average of more than 12,000 lizards per square mile. The discrep-
ancy is even greater than it appears, for Miller's study was made in a re-
gion where habitat conditions favor a denser population than does our
study area. For example, he (*loc. cit.*) mentioned seeing more than 100 liz-
ards in an area of 75 square yards, but the maximum number of lizards
we obtained at a single station at one time was 28. The smallest number
of lizards captured in one of our yearly surveys was 58 in 1950. This num-
ber is 1.93 lizards per acre or 1235 lizards per square mile and undoubt-
edly represents a minority of the lizards that actually were present in that
year (table 5).

Presumably the population is at its peak in the early autumn following
the birth of the annual brood in September and October, and is at its low-
est ebb just before this period, in late summer. Our estimates, being based
on the relatively inactive population in winter, probably represent a time
when the size of the population is slightly greater than its average size for
the year. Undoubtedly some mortality, especially among the newborn
young, takes place in late autumn, but more may occur in the following
spring when the lizards are most active.

REPRODUCTION

Most knowledge of the reproduction of *Xantusia vigilis* results from the

careful work of Malcolm R. Miller (1948a, 1951, 1954). Inasmuch as he studied lizard populations living within about 20 to 30 miles of our study area and in similar habitat, his findings are particularly pertinent to our work.

Xantusia vigilis is a viviparous lizard with a well-developed placenta (Heimlich and Heimlich, 1950). The number of young in a litter ranges from one to three, with a mean of 1.87 (calculated from data for 148 broods, in Miller, 1954, table 1). Ovulation takes place between early June and mid-July, the time depending on weather conditions, with ovulation being delayed in wetter, cooler years. Copulation precedes ovulation by from one to four weeks. The period of gestation is approximately 90 days, birth taking place in September or early October. Females of *X. vigilis* produce their first litter at an age of three years. The males mature in two years. The vast majority of reproductively active females produce two young; evidently there is no difference in the sizes of litters mothered by young or old females.

ANNUAL VARIATION IN REPRODUCTIVE SUCCESS

Miller (1954) recorded that in 1951 there was almost total failure of reproduction in the population he studied. Referring to lizards collected in the summer of 1951, he stated that "of the first 36 large and sexually mature females (having a snout-vent length of over 41 mm.) only two were gravid. The other 34 had either begun resorption of incompletely developed ova or had never achieved any degree of yolk deposition" (Miller, 1954, pp. 38–39). He had no difficulty in obtaining pregnant lizards in 1952.

Our data on annual variation in the production of young are taken from the estimates of numbers and ages presented and discussed in a preceding section. We assume that half of the lizards estimated to be three years of age or older are adult females, and use the ratio of young to adult females as an index of the success of reproduction in a given year. The indices range from 0.60 to 1.60 (table 4). We are aware of a variety of factors that may introduce inaccuracies, but there is no reason to believe that these factors change markedly from year to year, so the indices should be comparable. Though we refer to the numbers as indices, probably they are not very far removed from the true values (i.e., population parameters). For a year with complete reproductive success and no differential mortality between adult females and young in the time between parturition and sampling, the value calculated is 1.87. The observed value of 1.60 for 1952 is in good agreement.

Miller (1954) noted that the non-gravid females he collected in 1951

had markedly depleted fat bodies, which denoted a relatively poor state of nutrition. He believed that this state was the result of scarcity of food brought on by a very dry spring. If such is the case, a direct correlation between rainfall and reproductive success might be anticipated. The data presented in our table 6 and figure 18 reveal that there is a strong positive correlation. The year in which Miller found a dearth of gravid females (1951) was one of the poorest years in our series, and our best year (1952) was also a good year for the population that Miller studied.

RELATIONSHIP OF RAINFALL AND REPRODUCTION TO GEOGRAPHIC DISTRIBUTION

The presence of a strong correlation between rainfall and reproductive success could suggest that regions with an average rainfall near the lower

TABLE 6

ESTIMATED RATIO OF YOUNG-OF-THE-YEAR TO ADULT FEMALES OF *Xantusia vigilis* IN RELATION TO RAINFALL FROM NOVEMBER THROUGH APRIL (SEE FIGURE 18)

Year	Young per Female	Rainfall in Inches
1952	1.60	12.58
1954	1.17	7.56
1955	1.10	6.63
1953	0.88	6.63
1951	0.66	2.70
1950	0.60	2.20
Means	1.00	6.38

limit observed in our study area might not be capable of supporting *Xantusia vigilis*. That such is not the case is shown by the presence of the species in such relatively arid places as San Felipe, Baja California, and Desemboque, Sonora, both on the Gulf of California, and the Kofa Mountains near Yuma, Arizona.

An attempt to explain the geographic distribution solely in terms of rainfall ignores the probability that it is not rainfall as such but rather rainfall as it determines the abundance of invertebrates upon which the lizards feed that is significant for reproduction. In our study area there lives a constellation of invertebrate species that is well adapted to the prevailing climatic regime dominated by cold-season precipitation. When the winter rains are unusually sparse the invertebrate fauna does not flourish and the lizards produce few young, but such an occurrence does not happen often enough or in enough consecutive years to do permanent
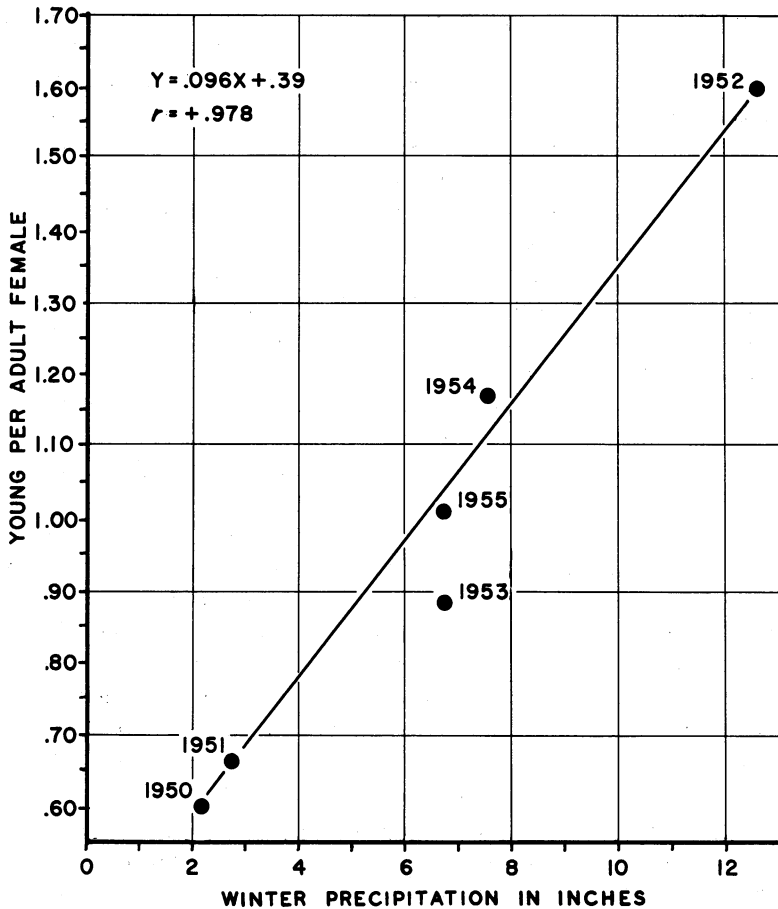
FIG. 18. Relationship of winter precipitation to production of young in *Xantusia vigilis.*

injury to the lizard population. The primary consumer invertebrate fauna of a region such as Desemboque is adapted to the drier climate of reversed seasonal precipitation (summer) and produces enough food for the lizards even though the rainfall may be markedly less than in some other parts of the range of *Xantusia.*

PREDATION

Apparently the only report in the literature of predation in nature on *Xantusia vigilis* is that of Banta ("1960" [1961]), who found an individual of *Xantusia* in the stomach of a collared lizard, *Crotaphytus collaris.* Prob-

ably this predator, which favors rocky habitat, does not occur in the immediate area where our study was made. Banta commented that the prey must have been active in the daytime to have been captured by *Crotaphytus*. When the difference in habitat selection and daily activity period of the two kinds of lizards is considered, it is doubtful that *Crotaphytus* is an important predator on *Xantusia*.

Persons searching for *Xantusia* occasionally encounter the night snake, *Hypsiglena torquata*. Stebbins (1948a, p. 99) and Miller (1951, p. 117) suggested that *Hypsiglena* may prey upon *Xantusia*, and Cowles (1941) noted that this snake feeds readily upon *Xantusia* in captivity. Johnson, Bryant, and Miller (1948, p. 267) recorded the close association of the snake and lizard in the debris of Joshua trees. We did not find *Hypsiglena* in our study area during the periods of winter census, as was expected, because snakes are not active there during the winter. *Hypsiglena* was, however, taken nearby during the summer months previous to the initiation of this work.

A number of potential predators among the mammals occur in the Joshua-tree habitat of *Xantusia*. Vaughan (1954) found the following species which we regard as potential predators in this habitat within 1 to 6 miles of our study area: grasshopper mouse (*Onychomys torridus*), badger (*Taxidea taxus*), coyote (*Canis latrans*), and kit fox (*Vulpes macrotis*). Miller (1951, p. 116) found *Xantusia* to be absent from the nests of the wood rat and thought that the lizard might be eaten by the rodent. Our experience was the opposite, for we found *Xantusia* abundant in the nests of *Neotoma lepida*, including nests that definitely were inhabited by rats.

Potential avian predators, such as the diurnal sparrow hawk (*Falco sparverius*) and loggerhead shrike (*Lanius ludovicianus*) and the nocturnal screech owl (*Otus asio*), undoubtedly occur is the study area, for these birds are regularly found in a habitat of Joshua trees, often nesting in the trees (Johnson, Bryant, and Miller, 1948). However, they do not seem to offer a serious threat to the *Xantusia* population, for the lizards, although they may be diurnal as well as crepuscular and nocturnal (Miller and Stebbins, 1964, p. 399), seldom venture out of the shelter of the logs of Joshua trees or the nests of the wood rats.

It seems likely to us that the principal predator must be the night snake. Undoubtedly other snakes, such as *Lampropeltis, Rhinocheilus,* and *Arizona,* capture an occasional individual of *Xantusia,* but none of these (or any other potential predator) is so regularly associated within the immediate habitat of the lizard as is *Hypsiglena*. This statement should not be taken to mean that *Hypsiglena* is restricted to the Joshua-tree habitat, for like *Xantusia* it has a wide geographic and ecological distribution. Al-

though *Hypsiglena* is probably the chief predator on *Xantusia vigilis,* it is doubtful that this snake, which is nowhere abundant, makes serious inroads on the lizard populations.

SURVIVORSHIP

The life table (table 7) is a so-called "vertical" table based on the average age structure shown in figure 17 and table 4. The survivorship curve taken from these data is plotted as A in figure 19.

As is pointed out in a foregoing section, the greatest errors probably are present in the estimates of age and numbers of very young and very old

TABLE 7

LIFE TABLE FOR *Xantusia vigilis* BASED ON ESTIMATED AVERAGE AGE STRUCTURE OF POPULATION

x Age in Years	d_x Number Dying in Age Interval out of 1000 Born	l_x Number Surviving at Beginning of Age Interval out of 1000 Born	1000 q_x Mortality Rate per 1000 Alive at Beginning of Age Interval	e_x Expectation of Life in Years
0–1	117	1000	117	4.04
1–2	144	883	163	3.52
2–3	144	739	195	3.10
3–4	93	595	156	2.73
4–5	136	502	271	2.15
5–6	116	366	317	1.76
6–7	127	250	508	1.34
7–8	35	123	285	1.22
8+	88	88	1000	0.50

individuals. If we assumed that, as an extreme example, the average adult population shown in figure 17 had 100 per cent of reproductive success (1.87 young per adult female), a survivorship curve with the new, larger proportion of young as the base of 1000 could be constructed. An additional assumption would be that the yearlings also were under-represented in the sampling. Curve B in figure 19 is constructed with this new base of 1000 and an arbitrarily augmented quota of yearlings. The curves are terminated arbitrarily at nine years.

Both curves are extreme and in a sense unrealistic. In curve A the number of young born is underestimated, and hence the curve shows too flat an initial segment. In curve B a higher natality than is likely is assumed, so the mortality is overestimated and the curve dips too steeply. Despite

their obvious deficiencies, the curves have the merit of setting reasonably low and high values of survivorship.

LONGEVITY

Many populations of lizards other than *Xantusia* apparently show a high rate of turnover, with virtually complete replacement in a year or two. Persons familiar with this sort of population may regard our calculations of survivorship in *Xantusia* as questionable, since we conclude that an individual of *Xantusia* at birth may have a life expectancy of four years. However, a consideration of the fecundity and age at maturity of *Xantusia* shows that the situation could scarcely be otherwise. A female *Xantusia* matures at three years of age and produces only two young per year. Thus, in order merely to replace herself and her mate (with no allowance for loss of young) she must survive for three years.

As examples of long-lived individuals, we have selected several lizards that were relatively large, hence presumably relatively old, when first captured and were known to have lived for several years after the initial capture. The ideal demonstration of maximum longevity would be based on individuals marked as young-of-the-year, but this was impossible because the seven-year time span of our study was shorter than the maximum age attained by many of the lizards.

One of the lizards in our sample, number 56, may have been more than 11 years of age at last capture. When first captured in December, 1949, the lizard measured 44 mm. and thus must have been at least four years old (fig.13). No further captures ensued until December, 1953, when the lizard (or another with the same toes missing) was captured at another station. The lizard was recaptured at the new station in December, 1954, December, 1955, and March, 1957. If only a single lizard is involved here, it had a minimum age of 11.5 years when last captured. However, because of the lapse of three years without capture and the apparent change of station, we suspect that natural loss of toes may have taken place and that two different lizards were handled. If the 1953–1957 captures were of a second lizard, it had a probable minimum age of eight and one-half years at last capture.

A minimum age of nine and one-half years is well established for lizard number 312. When first captured in December, 1952, the lizard measured 42 mm. Its minimum age at that time (fig. 13) might have been four years, but an age of at least five years is much more likely, because the two years preceding first capture, 1950 and 1951, were drought years in which growth was greatly curtailed. This lizard was captured at the same

station in each subsequent field session through March, 1957, by which time it had attained a length of 47 mm. If it be assumed that this lizard was born in September 1947, it was nine and one-half years old when last captured.

A probable age of eight years is indicated for three lizards. Two of these were 44 mm. in length, probably at least five years old when first captured, and were at the same respective stations three years later. Another lizard measured 39 mm. when first captured in 1952. If the two preceding years of poor growth are considered, an age in 1952 of four years is reasonable. This lizard was recaptured at the same station in each of the four succeeding field sessions, and was thus eight and one-half years of age in March, 1957, when last seen.

The sizes attained by the several lizards discussed in the preceding paragraphs indicate that they are females (see p. 22). It should not be inferred, however, that females necessarily live longer than males; rather, some bias against estimating similarly great ages in males is inherent in our methods. Consider, for example, lizard number 149. When first captured in 1950 it had a length of 42 mm. From a conservative interpretation of the growth curve of males (fig. 13), the lizard would be assigned a probable age of five or six years. The lizard was taken at the same station in 1951 and 1953 but was of the same size. The estimated age in 1953 is eight or nine years, but, as the lizard was a male that had reached maximum size by 1950, it is quite possible that it was older than five or six years when first captured in 1950. The general absence of a similar growth plateau in female lizards makes the underestimation of initial age somewhat less likely.

REGULATION OF NUMBERS

In the absence of much desirable data on the major causes of mortality in *Xantusia,* little can be said at this time as to what limits the numbers of lizards present. Predation may not play a vital role, but social antagonism acting when suitable habitat is limited may be important.

In order to survive the freezing conditions of winter, the lizards must be within or under logs of the Joshua tree that are large and well insulated or must find shelter in the nests of rats and similar piles of debris. Unquestionably, extremely cold conditions eliminate occasional individuals that do not find adequate shelter. We observed an occasional freshly dead individual during December, 1948, under some of the smaller logs of the Joshua tree in Walker Pass, Kern County, California, shortly after the passing of a severe cold front. The lizards are not antagonistic in winter, but are gregarious, often aggregating in large numbers (30–40) in the

most suitable situations in the habitat. In the spring and into the summer, however, fighting takes place, and the population is maximally dispersed. Seldom are more than two or three lizards found under the same shelter. Miller (1951, p. 115) reported that lizards are found almost exclusively under shaded cover in summer, for the temperature under unshaded cover often exceeds the maximum tolerable. A most critical time, then, appears to be during the heat of summer when territorial antagonism has forced some lizards into marginal and unsuitable habitats.

The area of habitat suitable for summer occupancy probably remains relatively constant. Therefore, summer heat and intraspecific territorial antagonism may act together as limiting factors in density-dependent fashion, i.e., the denser the population, the greater the numbers forced into marginal habitats. The indiscriminate action of low extremes of temperature in the winter would be density independent, as the absence of social antagonism in the winter permits individuals to aggregate in the relatively fewer suitable sites and not to be forced into marginal areas. Precipitation is a density-independent factor. When the winter precipitation is inadequate, nutrition suffers and fewer young are born (fig. 10, table 6).

POPULATION ECOLOGY OF *XANTUSIA VIGILIS* AND THAT OF OTHER LIZARDS COMPARED

Relatively little is known of the dynamics of lizard populations. For only a handful of species are there adequate data on reproductive potential and natality, and information on mortality rates and age distributions is even scantier. Certainly the best-known lizard is *Sceloporus olivaceus*, the subject of a study by Blair (1960). Because in reproductive potential and survivorship this species contrasts markedly with *Xantusia vigilis*, it is instructive first to compare these two before taking note of species bridging the demographic gap.

Xantusia vigilis has the lowest reproductive potential of any lizard so far studied. A female does not produce her first litter until three years of age. The usual number of young is two, there is only one brood a year, and old lizards are no more fecund than those in their first breeding season. Lizards of other genera, such as *Anolis,* may lay only one or two eggs per clutch but produce more than one clutch in a year. *Sceloporus olivaceus* has one of the highest, if not the highest, reproductive potentials known among lizards. Most females become sexually mature and breed at an age of less than one year. Even a yearling may produce four clutches of eggs in her first breeding season, and this number of clutches is typical of two-year-old and older lizards. Moreover, the average size of a clutch more

than doubles in three years, increasing from 11.3 in yearlings to 18.4 in two-year-olds and 24.5 in lizards three years of age. Thus, a female *Sceloporus* surviving to her third breeding season and laying an average number of eggs could produce about 217 young in the same length of time that a female of *Xantusia* would give birth to only two. Furthermore, in this time most of the young of the original female *Sceloporus* could mature and contribute to the population, producing an astronomical number of offspring.

Mortality is the other side of the coin. An average of about 75 per cent of the *Sceloporus* eggs fail to hatch. They are destroyed by predators or desiccate when rainfall is too infrequent to keep the nest site moist. The embryos of viviparous *Xantusia* are safe so long as the mother survives, though ova may be resorbed if food for the mother is inadequate. A newborn *Xantusia* has a life expectancy of about four years; a hatchling *Sceloporus,* one of about three months. Blair noted that about 80 per cent of the breeding population is replaced annually. For every 1000 *Sceloporus* eggs laid only about 250 hatch, and 40 lizards reach sexual maturity at one year of age. Perhaps as many as 300 to 600 of every 1000 *Xantusia* born survive for three years to reach sexual maturity.

Sceloporus u. undulatus, studied in Georgia by Crenshaw (1955), is similar to *S. olivaceus* in its high mortality rate, having a "maximum ecological life expectancy of . . . about three years, the average, something less than six months" (Crenshaw, 1951, p. 298). The reproductive potential is lower than that of *S. olivaceus,* with an average of eight eggs per clutch and probably two clutches per season. Maturity is reached in the first year of life. Kennedy (1958) studied *Sceloporus undulatus hyacinthinus* in Texas and found similar mortality. He estimated that there was an annual mortality of 77 per cent, that hatchlings have a life expectancy of about three months, and that about 6 per cent of them attain an age of one year. The maximum estimated age was 28 months.

Sceloporus occidentalis of the Pacific coastal states is a close relative of *S. undulatus.* Fitch (1940) estimated an annual replacement of 80 per cent in populations he studied, a figure similar to that found for *S. undulatus.* Evidently *S. occidentalis* produces only one clutch per year, but the average size of a clutch is larger (13.7 eggs) than in *undulatus.*

Since the mortality rates after hatching of these *Sceloporus* are rather similar, but their reproductive potentials somewhat dissimilar, it follows that the difference must be made up in mortality before hatching. *Sceloporus olivaceus* is adapted to conditions under which predation on the eggs (particularly by the patch-nosed snake, *Salvadora lineata*) or desiccation of the nest is likely to occur. Rainfall is typically highly erratic during

the nesting season. The laying of four clutches in a season increases the probability that some eggs will experience sufficiently moist conditions to permit hatching if they escape predation. There is no question of adequate rainfall in the nesting season of *Sceloporus occidentalis*, for there is little if any chance of rain. The discovery of the eggs of any lizard (not just *Sceloporus*) in the Pacific coast states is a rarity. Presumably the females usually nest deep underground in the burrows of rodents or other animals where there is sufficient moisture in the soil. The absence of rain in the summer months may restrict egg laying to the spring or the early summer when there is still sufficient residual moisture in the soil from the rains of winter and early spring.

A high annual replacement of individuals is not necessarily characteristic of *Sceloporus*, as the data of Stebbins (1944, 1948b) and Stebbins and Robinson (1946) for *Sceloporus graciosus* show. Stebbins (1948b) speculated that about 50 per cent of a population that existed in 1942 (exclusive of that year's juveniles) was replaced in two years, two-thirds in three years, and nine-tenths in five years. A number of lizards in the population were at least seven or eight years old. The reproductive potential of *graciosus* is low, as would be anticipated: one clutch per year averaging 3.33 eggs.

When one compares life span and annual replacement of several populations, the factor of yearly period of activity must be considered. It is difficult, for example, to make valid comparisons between a population of *Sceloporus graciosus* in which individuals are active only six months of the year with one of *S. olivaceus*, active for nine months. The longevity of *Xantusia vigilis* is all the more remarkable because these lizards (at least in the populations we and Miller studied) are active throughout the year, though activity is doubtless considerably restricted in winter. The best evidence of year-round activity is Miller's statement (1951, p. 116): "Stomach analyses showed that feeding occurs throughout the year."

A species of lizard similar in many ways to *Xantusia vigilis* is *Leiolopisma zelandica* of New Zealand, the subject of a comprehensive study by Barwick (1959). *Xantusia* and *Leiolopisma* are of somewhat similar habitus, though *Leiolopisma* is larger, up to 64 mm. from snout to vent as compared to 50 mm. in *Xantusia*. Both are viviparous and produce one brood a year. The newborn lizards are of similar size and weight: 23 mm. from snout to vent and 0.23 gram in *Xantusia* (Miller, 1951, p. 118) and about 26 mm. and 0.28 gram in *Leiolopisma*.

Xantusia and *Leiolopisma* differ markedly in growth rate. Though only slightly larger than *Xantusia* at birth, *Leiolopisma* reaches a length of 46 mm. in one year, a size that a female *Xantusia* does not reach for at least five years and that males may never attain. Both sexes of *Leiolopisma* ma-
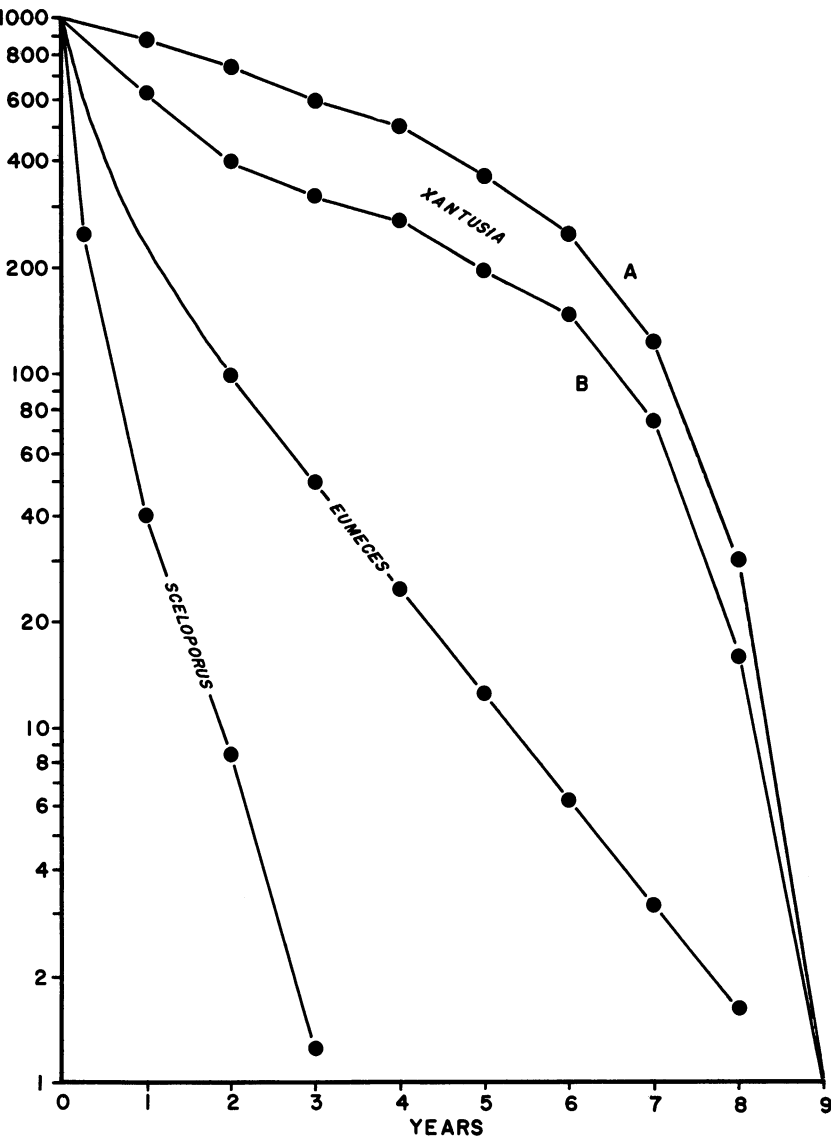
Fig. 19. Survivorship curves for *Xantusia vigilis, Eumeces fasciatus,* and *Sceloporus olivaceus;* see text for explanation of curves A and B.

ture in slightly less than two years, whereas males of *Xantusia* mature in two years and females in three. The growth of *Leiolopisma* is the more re-

markable, because this lizard undergoes more than four months of hibernation with little or no growth, while *Xantusia* is evidently more active in the winter (Miller, 1951, fig. 1).

Inasmuch as a female of *Leiolopisma zelandica* matures at two years of age and produces three to five young a year, the species has a higher reproductive potential than *Xantusia vigilis*. However, by more typical lacertilian standards *Leiolopisma* has a low potential and thus is more like *Xantusia* than like many other lizards.

Xantusia and *Leiolopisma* are similar in being sedentary. Juveniles of *Leiolopisma* move farther than adults, which have a home range with an average diameter of only 18 feet. Adults of *Xantusia* seldom leave the log pile or rat nest in which they live, and there is no indication that juveniles are more inclined to move than are adults.

Barwick's estimate of a population density of 900 per acre for *Leiolopisma* seems to indicate an immensely denser population than we encountered in *Xantusia,* for our highest estimate was 25 per acre. However, as Barwick pointed out (1959, p. 377), his animals were living in an area of ¼ of an acre of optimum habitat conditions. Our study area included vast stretches of terrain unsuited to the lizards. It might be more apt to compare the density of *Leiolopisma* with Miller's (1951, p. 116) record of more than 100 *Xantusia* seen in an area of 75 square yards, or more than 6400 lizards per acre. These observations point up the difficulty of making meaningful comparisons between species living in different areas and habitats, but do not obscure the essential fact that both species locally may achieve very high population densities.

It is evident that *Xantusia vigilis* and *Leiolopisma zelandica* are highly similar in many aspects of their ecology and life history. The similarities represent instances of parallel evolution in distantly related species.

The survivorship of three lizard populations is compared in figure 19. The curves for *Xantusia* are explained on page 43. That for *Eumeces fasciatus* is based on the data of Fitch (1954, pp. 140–141), who indicated that about one individual per brood of nine or 10 survives to adulthood at two years of age, and that "any given age group evidently is subject to annual reduction amounting to at least half its numbers." The curve for *Sceloporus olivaceus* is taken from data presented by Blair (1960, chap. 4), averaging the slight differences in survivorship of male and female lizards. The first change in the slope of the *Sceloporus* curve marks the time of hatching, reflecting the greater mortality rate before hatching.

The curves for *Sceloporus* and *Eumeces* resemble the Type-II diagonal curve characteristic of many birds (Deevey, 1947). The straight line (on a semilogarithmic plot) implies a constant rate of mortality; as Deevey

(1947, p. 310) wrote, "experience of life is of no use . . . in avoiding death." The curves for *Xantusia*, although having relatively straight diagonal sections, tend toward the Type-I curve, which describes a population in which most of the individuals live a relatively long time and the mortality is less evenly distributed through the life span of a cohort. An approach to a Type-III curve, with heavy initial mortality followed by a period of greatly reduced mortality rate, is seen in the curve for a small population of *Crotaphytus collaris* published by Fitch (1956, p. 265). The young and subadults are particularly vulnerable, but adults established in their territories are relatively secure.

The comparisons made in this brief section indicate something of the extremes attained by lizards in their life histories, with particular reference to reproductive potential and survivorship. Mode of adaptation does not necessarily follow taxonomic lines: *Sceloporus olivaceus* is at one extreme and *Xantusia vigilis* at the other, but if a survivorship curve could be constructed for *Sceloporus graciosus* it probably would resemble that of *Xantusia* more than it would that of *S. olivaceus*. The skink *Leiolopisma zelandica* probably would show a curve much like that of *Xantusia* in contrast to the straight diagonal curve of another skink, *Eumeces fasciatus*. A subject virtually untouched as yet is the comparative population ecology of conspecific populations living in vastly different environments. For example, *Xantusia vigilis* lives in the Sonoran Desert near sea level on the shores of the Gulf of California and at an elevation of over 9000 feet in the Panamint Mountains of California (Turner and Wauer, 1963, p. 125). It would be of great interest to compare the ecology of lizards living in these regions with that of the population we studied.

It is perhaps not entirely coincidental that the three lizards of which the survivorship curves are shown in figure 19 differ with respect to the care that they provide their young. *Sceloporus* produces a large number of eggs and provides no care other than burying them in a suitable spot. *Eumeces* lays fewer eggs and remains with them, offering them some protection. *Xantusia* has the lowest reproductive potential and is viviparous.

SUMMARY

Over a period of seven years we studied a population of desert night lizards, *Xantusia vigilis*, in the Antelope Valley part of the Mohave Desert in southern California. These secretive lizards inhabit decaying stumps and fallen trunks and limbs of Joshua trees (*Yucca brevifolia*), nests of wood rats (*Neotoma*), and similar surface litter. On visits to the study area during the winter, seven times in December and once in March, when the lizards aggregate and are relatively easy to collect in large numbers, we cap-

tured 656 lizards and marked them by clipping toes before releasing them. We recaptured 152 marked lizards a total of 216 times. General observations made during the field surveys, together with data on growth, longevity, and movements derived from the recaptured individuals, form the basis for this report.

Xantusia vigilis is viviparous and produces only one to three young, usually two, in a litter. The annual brood in the Antelope Valley region is born in September in most years, with births taking place as late as October on occasion. At birth the lizards average 23 mm. from snout to vent, ranging from 21 to 25 mm. Little growth takes place before the winter period of relative inactivity. In December of the year following birth, at an age of about 15 months, the lizards average 29.6 mm. from snout to vent. Recaptured individuals of known age ranged in length from 26 mm. to 32 mm., but in a particuuarly poor year probably even less growth may take place.

By the third December following birth, at an age of about 27 months, the lizards average 35.1 mm. in snout to vent length, ranging from 32 to 38 mm. At the end of slightly more than three years of life the average length is 38.4 mm., range 36–41 mm. Growth rate has decreased considerably, and there is considerable overlap in sizes of individuals comprising samples of two-year-old and three-year-old lizards.

The growth rates of male and female lizards evidently diverge in or before the fourth year of life. Females, on the average, add 1.5 to 2.0 mm. to their snout-to-vent length in each year after the third, and eventually may reach a length of 50 mm. The average annual increment for males after the third year is about 0.5 mm., with a maximum size attained of about 42 mm. to 44 mm. Some individuals cease to grow at a length as short as 38 mm. The amount of growth, particularly in the early years of life, appears to be correlated directly with rainfall which presumably determines the abundance of food.

The majority of *Xantusia* that survive to adulthood lose the tail at least once. Undoubtedly some losses are caused by predators, but, in view of the lack of other evidence of severe predation, we infer that most instances of autotomy stem from intraspecific fighting. Regeneration can be virtually perfect, and a well-regenerated tail may be distinguishable from an original one only through an examination (such as by X-ray) that reveals replacement of the original vertebrae by a cartilaginous rod. In autotomy, a lizard may give up as much as 22.6 per cent of its total body weight. There is some evidence that regeneration of the tail reduces the growth rate of young lizards.

Suitable habitat is discontinuously distributed; lizards seldom leave

the shelter of their logs or rat nests and take up residence elsewhere. In a total of 216 recaptures of 152 lizards, some as long as five to six years later, only 19 times were lizards found to have changed residence. The mean distance moved was 353 feet, range, 36 feet to 1050 feet.

We estimate that an average of 518 lizards (range, 302 to 680) inhabited the 27-acre study area during the period of our winter surveys—about 19 per acre or 12,000 per square mile. These figures are crude approximations and undoubtedly err on the low side. A large percentage of the population, about 50 per cent on the average, is composed of adult lizards—males two years or more in age, females three years or more.

In unusually dry years many and perhaps most of the female lizards produce no young, presumably because of inadequate nutrition stemming from a scarcity of the invertebrates upon which the lizards feed. The correlation of winter precipitation with reproductive success (with the use of the ratio of females to young in the winter population as an index) is strong: $r = + 0.978$.

As might be anticipated for a species in which the females do not mature until three years of age and produce only two young per year, *Xantusia vigilis* has a long average life span. The average life expectancy at birth may be as high as four years, and individuals live for at least nine years, probably longer.

Predation is thought not to be significant in population control. Social antagonism causes territorial deployments within the populations during the spring and hot summer months. If shelter is inadequate, heat and antagonism may act together in density-dependent fashion as limiting factors. Unusually cold weather in the winter may find some lizards insufficiently sheltered, though at this season most individuals aggregate in favorable sites.

In comparison with other lizards, *Xantusia vigilis* shows a high life expectancy at birth, slow growth, late maturity, and low reproductive potential—perhaps the lowest known among lizards.

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