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A DISTRIBUTIONAL ANALYSIS OF EPIGEAN POPULATIONS OF *EURYCEA NEOTENES* IN CENTRAL TEXAS, WITH COMMENTS ON THE ORIGIN OF TROGLOBITIC POPULATIONS

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ABSTRACT: Epigean populations of the salamander *Eurycea neotenes* are restricted to the dissected southern margin of the Edwards Plateau of central Texas, with peripheral isolates on the western and northeastern limits of the Balcones Fault Zone. Populations are confined to thermally stable (18–21 C), temporally reliable spring habitats. Reliability is a function of groundwater recharge area and storage volume, and can be estimated by measuring local topographic relief. A survey of 140 springs shows that this measure is positively correlated ($r = 0.93$) with the proportion of springs inhabited by salamanders; thus, local relief data can be used to estimate the probability that salamanders occupy unsurveyed springs. Application of this index to all mapped springs in and adjacent to the known distribution of *E. neotenes* gives an estimate of 563 populations. Corrections for mapping bias place the probable number in the range 788–1543. The index and related geologic and hydrologic data also indicate that springs outside the known distribution are not suitable for habitation by *E. neotenes*. Troglobitic populations originate when springs fail, and they are most numerous on the eastern limb of the Plateau where temporally reliable springs are few.

Key words: Amphibia; Caudata; Plethodontidae; *Eurycea neotenes*; Texas; Edwards Plateau; Distribution; Troglobites

THE location and geology of the Edwards Plateau of central Texas render that region a center of endemism and relictual populations for plants (Correll and Johnston, 1970) and animals (Blair, 1950; Mitchell and Reddell, 1971; Remington, 1968) derived from southeastern, neotropical and southwestern regions. The extensive, horizontal limestones of the Plateau have been thoroughly dissected by drainages, radiating from the high and level northwestern quadrant, wherein mesic floral and faunal elements interdigitate with arid elements restricted to the rocky, well-drained divides. The persistence of mesic relicts owes largely to the role of the Plateau limestones in collecting, transmitting and releasing large quantities of water in a temporally reliable fashion. This groundwater discharges in numerous springs in headwater canyons and along the broad curve of the Balcones Fault Zone, a major structural feature which sharply delimits the uplands of the Plateau from the coastal plain to the east and south.

The springs of the Edwards Plateau and their associated subterranean drainages are inhabited by relict populations of hemidactyliine plethodontid salamanders of the genera *Eurycea* and *Typhlomolge*. Distributional restriction, paedomorphosis and the colonization of caves are dominant themes in this assemblage and can be viewed as successive elements of an evolutionary response to progressive environmental deterioration. I have previously argued that the Edwards Plateau presents few microhabitats suitable for metamorphosed hemidactyliines, and that selection for paedomorphosis is enhanced during episodic droughts which eliminate surface streams and most springs. Further, paedomorphosis and forced residence in subterranean refugia preadapt populations to the eventual colonization of caves, which occurs when erosional processes bring about the definitive cessation of flow in isolated springs (Sweet, 1976, 1977).

This interpretation of the evolutionary history of the central Texas hemidactyliines depends on an understanding of the processes that force distributional restriction on epigean (surface-dwelling) populations. The present account details the distribution of epigean populations of the widespread species *Eurycea neotenes* and seeks to identify determining factors in the geomorphology and hydrology of the Plateau with emphasis on evaluating variation in the temporal reliability of spring habitats. It is not sufficient to enumerate localities; rather, one would like to know what proportion of springs are habitable for *E. neotenes*, and what may be wrong with those that are not. I approach this topic through consideration of correlates of the presence or absence of salamander populations in 140 springs examined in the field. Emergent generalizations bear directly on the problem of distributional restriction and provide a means of estimating the probability that a given spring is habitable. From the latter, I derive estimates of the number and regional density of populations of *E. neotenes* and evaluate the likelihood that populations occur outside the presently known range. These data are relevant to any distributional analysis but are difficult to acquire directly.

Materials and Methods

Fieldwork was conducted in June 1969, June and July 1970, July and August 1971, June through September in 1973 and 1974, and in June 1977. A total of 3300 specimens of *E. neotenes*, representing 83 epigean populations, was collected during this period, augmented by about 500 specimens borrowed from other collections, representing at least 17 additional localities. The localities, specimen numbers and repositories of these series are listed Appendix I. Detailed field notes are on file in the Museum of Vertebrate Zoology, University of California, Berkeley.

Locality and topographic data were taken from U.S. Geological Survey 7½′ maps (USGS, 1979). In addition to data for springs examined in the field, topographic information was collected for all other springs marked on 468 of the 478 7½′ maps (10 quadrangles not mapped) in the area indicated in Fig. 1A. This region encompasses the major part of the Edwards Plateau and Llano Uplift as well as the Balcones Fault Zone and the adjacent Gulf Coastal Plain. The known distribution of the *Eurycea* in Texas comprises about 127 7½′ quadrangles roughly centered within this polygon.

Geologic data derive from direct examination in the field, and from Stricklin et al. (1971), Rose (1972), and the county groundwater resources publications of the Texas Water Development Board, Austin (TWDB, 1976).

Results and Discussion

Distribution of Epigean Populations

Distributional information, summarized and expanded by Baker (1961), comprises much of the early literature concerning *Eurycea neotenes*. Few new localities have been reported in recent years. A general outline of the range of epigean populations was provided by Sweet (1976, 1977), but localities were not indicated for the major portion of the suggested range. Fig. 1B conveys this information for 100 populations, whose locations are given in Appendix I. A maximum of 37 additional populations (not mapped) may be represented by specimens with inadequate data housed in various collections (listed in Sweet, 1978, Appendix II).

Known populations of *Eurycea neotenes* are restricted to the dissected southeastern region of the Edwards Plateau, becoming closely confined to its coastward margins in the northeast and far west. Populations of *E. neotenes* are uncommon and appear to consist of few individuals on the Jollyville Plateau to the northeast of the Colorado River, in marked contrast to observations made elsewhere in the species' range. Three to seven unproductive visits often separate collections of single individuals or small series from springs in this area, whereas

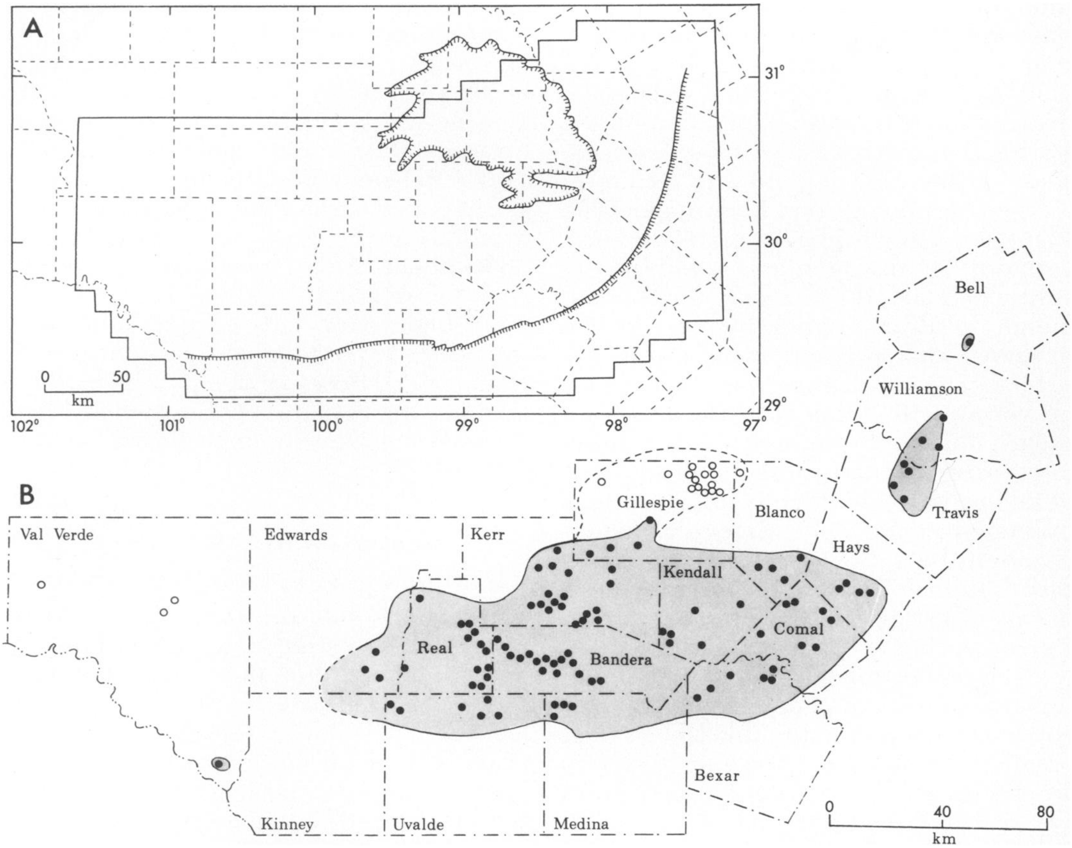

FIG. 1.—(A) Geography of the Edwards Plateau of central Texas. County outlines on the Plateau are indicated, and the margin of the Balcones Fault Zone and the Llano Uplift are marked by hatchured lines. A continuous line marks the limits of the polygon surveyed on topographic maps (see text). (B) Distribution of epigean populations of *Eurycea neotenes* on the Edwards Plateau. Counties are outlined. Filled circles mark known populations; open circles denote springs potentially suitable for *E. neotenes* as discussed in the text. The shaded area within a solid contour line approximates the predicted range of *E. neotenes*; a dashed contour line indicates regions where populations may also occur.

numerous individuals are nearly always present (when the spring is flowing) at sites in the major portion of the range to the south and west. This group of northeastern populations is apparently an isolate. The factors controlling this situation are suggested below.

Populations of *E. neotenes* are moderately common, though seldom large, in the eastern half of their main range, from the Blanco River in central Hays County westward to eastern Kerr and Bandera counties. Here they occur in streamside resurgences and headwater springs in the heavily eroded outlying remnants of the main Plateau surface, and in the springs associated with the Balcones Fault Zone. Populations become abundant and comparatively large in the rugged west-central portion of the range, between the headwater canyons of the Guadalupe and Nueces rivers. Both the number and the proportion of springs inhabited by *E. neotenes* peak in this region, as documented below, and it is the only area where metamorphosis occurs in these usually paedomorphic salamanders (Sweet, 1977).

Springs become uncommon to the west of the Nueces drainage, and those which exist are now heavily modified by human activity. Only one population of *E. neotenes* is known to occur to the west of southeastern Edwards County, inhabiting one of several outlets of San Felipe Springs in southeastern Val Verde County near the western terminus of the Balcones Fault Zone.

Restriction to Springs

Field experience indicates that epigean populations of *Eurycea neotenes* are restricted to the vicinity of springs at least during the summer months (comparable data are not available for other periods). While occasional individuals may be found over 25 m from any evident spring, each of the 85 populations located was closely associated with one or more spring exits. Springs provide a combination of conditions that are unique among aquatic environments on the Edwards Plateau, including temporal reliability, thermal stability and minimal siltation and cementation by carbonate deposits in the gravel beds inhabited by the salamanders.

The thermal stability of springs may be critical during the summer months, when water temperatures in the exposed, shallow streambeds of the Plateau frequently exceed 30 C (Fig. 2; Goines, 1967). In contrast, spring temperatures approximate the mean annual temperature of a region (Meinzer, 1940). On the Plateau, springs range from 18–22 C, essentially without annual variation (Fig. 2; Brune, 1975; Goines, 1967). Hemidactyliine salamanders are generally associated with cool water temperatures (Brattstrom, 1963; Spotila, 1972), with the upper limits of their preferred thermal range roughly coincident with spring temperatures on the Plateau. As indicated by Fig. 2, it should be emphasized that these are the coolest waters consistently available during the period from May through September.

The distribution of water temperatures

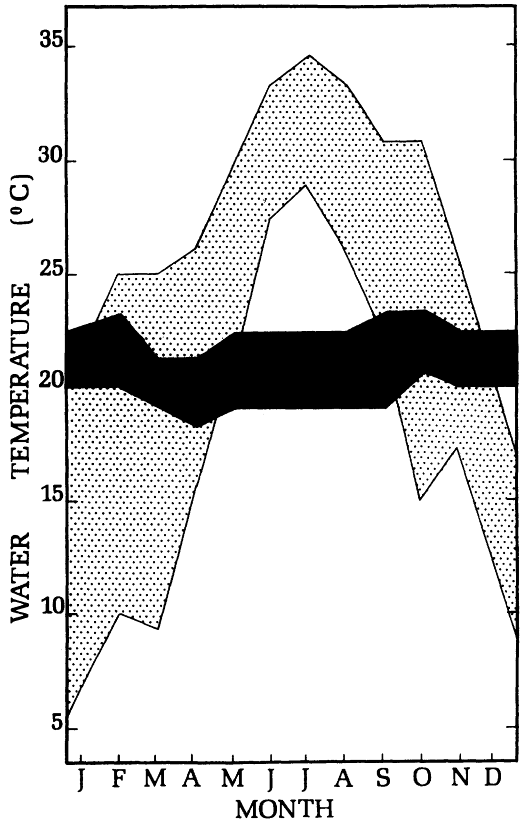

FIG. 2.—Comparison of the ranges of annual fluctuations in temperature for a typical Edwards Plateau stream (stipple), and for a large number of springs on the Plateau (black). Stream values are for the Blanco River at Wimberley, Hays County, between 1950 and 1966 (Goines, 1967); spring temperature data derive from sites throughout the Plateau as reported in publications of the Texas Water Development Board, Austin.

at 30 sites, where one or more specimens of *E. neotenes* was collected, is shown in Fig. 3. Most data points represent discrete spring populations. The higher values derive from three collections made downstream from springs. While downstream habitats were not examined as thoroughly as were spring exits, salamanders were regularly sought while approaching springs, and the observed association between temperature and occurrence seems to be real. Most of the dispersion in Fig. 3 reflects local varia-

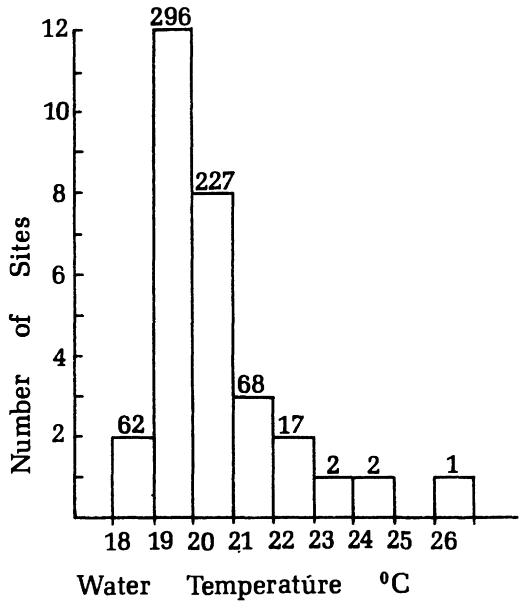

FIG. 3.—Frequency distribution of water temperatures at 30 sites of collection of one or more individuals of *Eurycea neotenes*. Numbers above each column indicate total numbers of individuals collected in each temperature interval.

tion in spring temperatures rather than the regular occurrence of salamanders downstream from spring exits.

An instructive example of this microhabitat restriction was noted on 4 September 1973 on the Clear Fork of Cibolo Creek in northeastern Bexar County. Water temperatures of 27–30 C were recorded during an unsuccessful search of this shallow, gravel-bottomed stream; eventually two small springs (19.5 C) were located by thermometer transects of the streambed across the trace of a small fault, and a series of 85 *E. neotenes* was collected by dredging the gravel at these points. No salamanders were found more than 0.5 m from either submerged spring exit, and those that escaped capture were observed to move toward the exits before burrowing into the gravel. This site is unusual in that spring locations are typically determined by rock strata rather than by faults, and because most small streambeds are dry except in the immediate vicinity of springs.

Geologic Correlates of Spring Location and Reliability

The limestones of the Edwards Plateau are not uniform in their abilities to store and transmit water. Only one stratum with broad surface exposure consistently carries substantial amounts of water, to the extent that springs occur in nearly every canyon transecting it. This 22–28 m thick layer of dense limestone, honeycombed with invertebrate burrows, is termed the Burrowed Member of the Fort Terrett Formation. It and its unnamed lateral equivalent in the Devils River Formation are underlain by impervious strata and lie 8–12 m above the base of the Edwards Group limestones throughout the Plateau exclusive of the Balcones Fault Zone (Rose, 1972). The majority of springs inhabited by *Eurycea neotenes* on the Plateau proper are those developed in this stratum; 85 (61%) of the 140 springs examined on the Plateau occur in the basal Fort Terrett and Devils River formations, and 67 (79%) of these springs contained populations of *E. neotenes*. In contrast, only 18 (33%) of the 55 examined springs arising from other strata were found to contain salamanders, and in 17 cases these sites lie in regions where the Edwards Group limestones have been eroded away. This distinction may be due to the high temporal reliability of springs developed in the former zone, which supports a distinct band of mesic vegetation that has been employed in constructing geologic maps from aerial photographs (Rose, 1972).

A more general analysis of the importance of this stratum in the location of springs may be approximated from topographic maps. For example, examination of four quadrangles in northwestern Real County (Joy Hollow, Jo Jan Van Camp, Bee Cave Hollow and Owl Hollow; 14L, 14M, 15L and 15M of Appendices III and IV) shows that 67 of 99 mapped springs lie in the elevational range of the basal

Fort Terrett (555–577 m, Rose, 1972), a band which comprises only 1.4% of the mapped area.

The development of springs in the Balcones Fault Zone along the margin of the Plateau is under structural as opposed to stratigraphic control (MacLay, 1974); the recharge characteristics and reservoir capacities of these springs are such that flow rarely or never ceases (Brune, 1975). Most of the large springs of the fault zone contain populations of *Eurycea* allied to *E. neotenes,* whose taxonomic allocation remains unresolved.

Topographic Correlates of Spring Reliability

Eurycea in Texas depend on the reliability of water sources as a consequence of paedomorphosis. Epigean populations are restricted to springs, and are isolated from other populations by varying (and often considerable) distances of unsuitable habitat types. Springs on the Plateau show a wide range in temporal reliability. Some rarely cease flowing, such as the major springs of the Balcones Fault Zone and those in canyons draining the main Plateau surface; others, left above the present groundwater surface by erosional lowering of valleys or located in strata with poor water transmission characteristics, flow only briefly after periods of heavy recharge. Most of the springs inhabited by *E. neotenes* lie between these extremes and may cease flowing for short periods during dry seasons, requiring the resident populations to withdraw temporarily into the subterranean drainage supplying the spring (Sweet, 1977). If this reservoir is inadequate, populations may become extinct, with recolonization uncertain.

Populations of salamanders were apparently absent from a number of springs investigated in the field. Many of these springs were noted to be in areas of low topographic relief or high on divides, or in other situations with unreliable recharge characteristics. Such springs might be prone to more frequent or prolonged failure than salamander populations could withstand. The aquifers supplying springs on the Plateau proper are of variable areal extent, and in general they correspond in size to the amount of adjacent land surface which is above the level of the local water table. This available recharge area and its reservoir capacity are directly related to the temporal reliability of the springs through which the aquifer discharges. Because the Plateau limestones erode to a constant slope, local topographic relief provides a good index of the size of an aquifer and can thus serve as an estimator of spring reliability. This measure is defined as the topographic relief from the spring to the highest point within a 1 km radius (excluding values for regions across canyons with lower elevations than the spring). The assumptions made in this model are met by all springs on the Plateau proper except streamside resurgences but are not valid for the major springs of the Balcones Fault Zone. The analysis below is limited springs of the former category.

These data include 85 springs on the Plateau known to be inhabited by *Eurycea neotenes* and 55 springs in which no salamanders could be found (Appendices I and II). Frequency distributions of these springs with respect to local topographic relief are shown in Fig. 4. Mean relief values are 76.2 and 53.0 m for inhabited and uninhabited springs, respectively; the two distributions are significantly different by Kolmogorov-Smirnov two-sample test (df = 2, $\chi^2 = 20.52$; $P < 0.001$). Greater local topographic relief correlates positively with the likelihood that a particular spring will be inhabited by *E. neotenes,* presumably through the association postulated between local relief and spring reliability.

The proportion of inhabited springs increases in a regular fashion with increasing topographic relief (Fig. 5). This relationship can be generalized to yield a probability function which can be employed to evaluate the likelihood that springs that were not examined in the

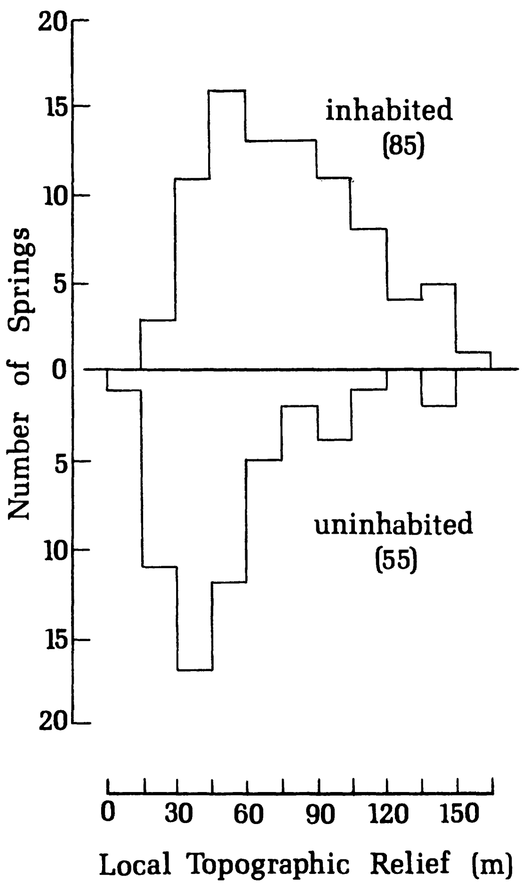

FIG. 4.—Frequency distributions of springs having and lacking populations of *Eurycea neotenes* with respect to maximum topographic relief within a 1 km radius of each spring (see text).

field contain populations of *E. neotenes*. This equation is:

$$P = 0.634(\log R) - 0.531 \quad (r = 0.93)$$

where P is the probability of habitation and R is local topographic relief (in meters).

General Analysis of Abundance and Distribution

A survey of 468 7½′ topographic maps, covering the known distribution of *Eurycea neotenes* and surrounding areas, shows a total of 1072 springs, 826 of which are located in the 127 quadrangles encompassing the presently known range. The numbers of marked springs per quadrangle are indicated in Appendix III. Regional variation in the density of springs is apparent, and is closely correlated with the geologic and topographic criteria discussed above. Low relief and the erosional removal of Edwards limestones contribute to the relative scarcity of springs on the eastern limb of the Plateau, from which the isolated Edwards cap of the Jollyville Plateau (F31, G30, 31) is clearly demarcated. Density of springs increases on the E-W trending divides of the Pedernales, Guadalupe and Medina rivers, and peaks in the rugged west-central region of N-S trending divides of the Sabinal, Frio and Nueces rivers. Farther north and west erosion has yet to expose the base of the Edwards limestones and springs are correspondingly few. Overall, springs are about 10 times more numerous per unit are within the known range than in the adjacent peripheral zone. Further, springs within the known range have greater local topographic relief ($\bar{x}$ = 88.2 m) than do the peripheral springs ($\bar{x}$ = 49.5 m).

The distributions of within-range and peripheral relief values transformed to probabilities of habitation are shown in Fig. 6. The two distributions are distinct: only 1.2% of the within-range springs have <30% probabilities of habitation, compared to 13.8% of the peripheral springs; conversely, 52.5% of the within-range springs have >70% probabilities of habitation, contrasted with 9.3% of the peripheral springs. The mean probabilities of habitation for springs in each of the surveyed quadrangles are shown in Appendix IV. Regional variation follows the same general pattern as the density of springs, though the Jollyville Plateau and E-W divides are not prominent. The region of greatest density of springs also shows consistently high probabilities of habitation, indicating a greater density of populations of *E. neotenes* here than elsewhere in its range.

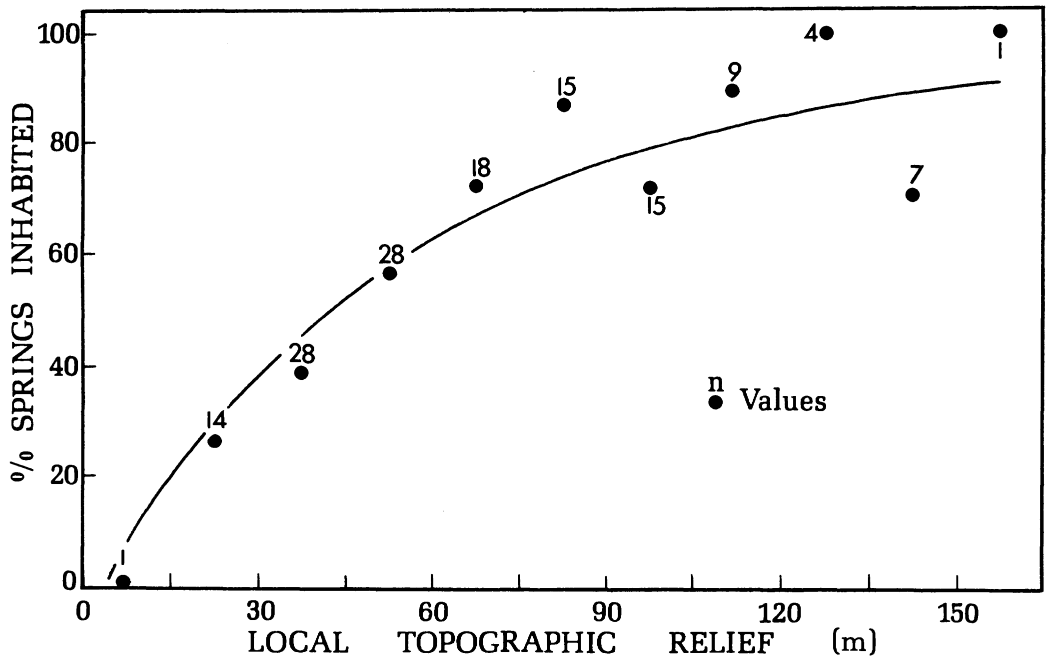

FIG. 5.—Relationship between local topographic relief and the proportion of springs found to be inhabited by *Eurycea neotenes*. The heavy line is the probability function $P = 0.634(\log R) - 0.531$.

Two general applications of these results are possible within the scope of the assumptions made: (1) an estimation of the number of populations of *E. neotenes* present within the known range, and (2) an evaluation of the possibility that the actual range of the species is more extensive than is presently known. The first application consists of an approximation derived from the summed products of the numbers of springs in each probability interval of Fig. 6 and the mean class probabilities of habitation. This yields an estimate of 563 populations based on mapped springs alone, a minimum number because a proportion of springs are not indicated on topographic maps. A partial correction can be derived from the observation that 56 (40%) of the 140 springs on the Plateau located in the field are not mapped; correction for mapping bias gives an estimate of 788 populations. This remains a conservative figure in that springs were initially sought by reference to maps, unmapped springs being located fortuitously in the course of fieldwork. An upper estimate of the actual number of unmapped springs can be derived from the observation that a spring is found in virtually every canyon that intersects the base of the Fort Terrett or Devils River formations (Rose, 1972; pers. obs.). Examination of the four quandrangles cited above shows that 195 canyons cross this horizon, but only 67 (34.4%) have mapped springs at this point. Thus, only about one third of the probable number of springs may be shown on topographic maps. Assuming that approximately 80% of all basal Fort Terrett-Devils River springs have populations of *E. neotenes*, as suggested above, the initial estimate of 563 populations should be increased by a factor of 2.74 (=1543) to provide an upper estimate of the number of extant populations. Most of these predicted localities lie in Real, western Bandera, and southeastern Edwards coun-

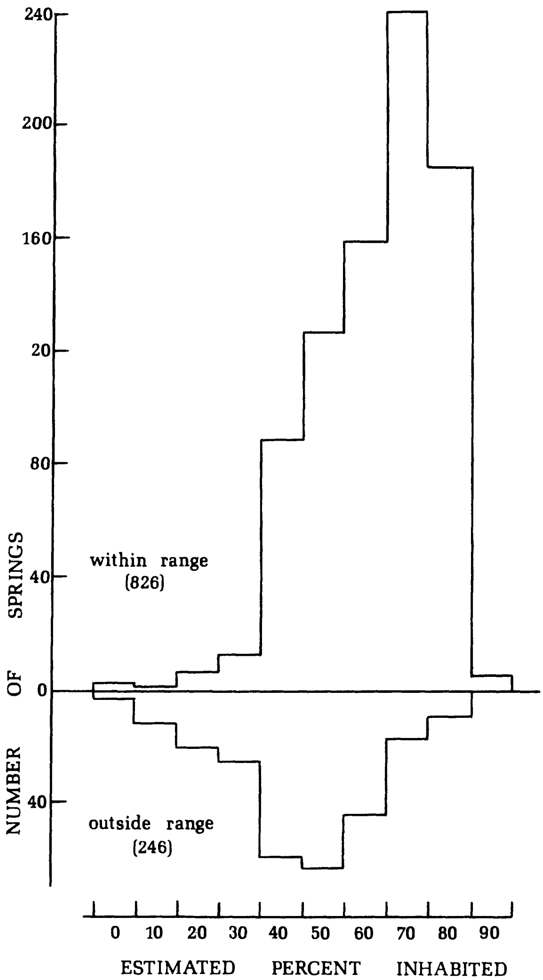

FIG. 6.—Frequency distributions of the probabilities of habitation (see text) for 1072 mapped springs within the polygon indicated in Fig. 1A. The zero line separates springs within the known range of *Eurycea neotenes* from those in surrounding areas.

ties, where the major drainages have developed very low gradients 10–50 m below the basal Edwards Group. For this reason, even the smallest tributary canyons transect the principal aquifer and should contain springs suitable for *E. neotenes*. To the east, the major streams have cut far below the basal Edwards and only the headwaters of large tributaries intersect it, if it is present at all.

A comparably derived estimate of the number of populations of *E. neotenes* that might occur peripheral to the known range yields 169 populations (incorporating correction for a 40% mapping bias). This estimate is probably incorrect for several reasons, the most basic being that the probability function indicates only the suitability of springs. Actual habitation depends on the probabilities of colonization or recolonization in the past and on the existence of continuously suitable conditions since the time of distributional restriction to springs. If recolonization is a common phenomenon, the distinction evident in Fig. 4 would not be expected. Further, the probability of recolonization is dependent on distance from a source population and is thus a variable factor. Some criterion of continuous habitability might estimate the likelihood of the existence of distant peripheral populations better than an unmodified probability summation.

An arbitrary criterion of ≥70% probability of habitation (≥79 m local relief) may be selected as the limiting value for continuously habitable springs. Satisfying this restriction are 433 (52%) of the mapped within-range springs and 26 (10.6%) of the mapped peripheral springs. In terms of 7½′ quadrangles, 34 of 127 within-range and 5 of 301 peripheral quadrangles are admitted (Appendix IV). Peripheral springs of ≥70% probability of habitation occur in three regions at varying distances from the known range limits of *E. neotenes* (distant west, adjacent north, and distant north).

Three springs in northern and central Val Verde County (quadrangles 1K, 6K and 6L of Appendices III and IV, indicated by open circles on Fig. 1B) satisfy all criteria of the model and may still contain populations of *E. neotenes* if the salamanders once occurred in the area.

Sixteen springs with ≥70% probability of habitation are mapped along the southern tributaries of the Llano River in northern Gillespie County (quadrangles 20H, 23–25H and 25G of Appendices III and IV, indicated by open circles on Fig.

1B), and others probably occur in the adjacent (unmapped) eastern part of Kimble County. This region of high spring density is contiguous with the known distribution of *E. neotenes*, and populations may occur in the area indicated by a dashed margin in Fig. 1B. However, many of these springs are situated in metamorphic strata of the Llano Uplift below the eroded rim of the Edwards Plateau, and no salamander populations have yet been located. These and seven other high-probability springs, located along the Colorado River in Llano, Burnet, San Saba and Lampasas counties (quadrangles 26C, D and F of Appendices III and IV, not indicated on Fig. 1B), do not satisfy the assumptions of the model, which is based on the hydrologic characteristics of the uniform limestone strata of the Edwards Plateau. The hydrology of the heterogenous, intensely faulted Llano Uplift is complex (Alexander and Patman, 1969; Barnes et al., 1972) and available information (Mount, 1962, 1963) suggested that springs on the Llano Uplift are less temporally reliable as a class than are springs on the Edwards Plateau. For this reason, the occurrence of a significant number of populations of *E. neotenes* on the Llano Uplift seems unlikely.

In conclusion, the actual distribution of epigean populations of *Eurycea neotenes* appears to coincide with the presently known range. Extensions are possible, but unlikely, in western Val Verde and northern Gillespie counties. The major part of the range occupies the dissected margin of the Edwards Plateau, populations being most numerous where erosion has exposed the basal units of the Edwards Group limestones adjacent to upland areas offering large groundwater catchment and storage capacities. Closer to the edge of the Plateau, the basal Edwards is absent or perched high on divides. Springs are fewer and less reliable, and populations of *E. neotenes* are much less common, in the regions where Glen Rose limestones are exposed. The isolated Edwards outcrop, which comprises the Jollyville Plateau to the north of the Colorado River, provides suitable recharge characteristics and supports populations of *E. neotenes* that are disjunct from the principal distribution. Other isolates occur in springs of the Balcones Fault Zone from Bell County in the northeast to Val Verde County at the western limit of the Plateau. These populations inhabit artesian springs recharged by the major rivers of the Plateau, and are consequently buffered against all but the most severe droughts.

Epigean populations of *Eurycea neotenes* are being eliminated from the coastward portions of the Plateau outside of the fault zone as erosion reduces the temporal reliability of springs. On a geologic time scale, the distribution will retreat to the northwest as extensions of the headwaters of the Plateau drainages intersect water-bearing strata, leaving troglobitic populations in their place. At present, troglobitic populations occur almost exclusively in the fault zone and areas immediately inland (Sweet, 1976), where Edwards Group limestones are downfaulted or absent, and temporally reliable springs are infrequent. Although caves with flowing water occur widely in Edwards Group limestones, only three of 30 known troglobitic populations occupy such caves. In two cases (Tucker Hollow Cave, Real County and Carson Cave, Uvalde County) the caves are former springs developed in the basal Edwards; Haby Water Cave (Bandera County) contains the only known troglobitic population occupying a cave in the upper Edwards Group limestones. The preponderance of troglobites on the eastern limb of the Plateau is consistent with the hypothesis that cave colonization follows the failure of springs. This point also reinforces the emphasis of the preceeding discussion of the importance of variation in the temporal reliability of spring habitats to the current distribution of epigean populations of *Eurycea neotenes*.

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Literature Cited

Alexander, W. H., Jr., and J. H. Patman. 1969. Ground-water resources of Kimble County, Texas. Texas Water Devel. Board Report 95, Austin.

Baker, J. K. 1961. Distribution of and key to the neotenic *Eurycea* of Texas. Southwest. Nat. 6:27–32.

Barnes, V. E., W. C. Bell, S. E. Clabaugh, P. E. Cloud, Jr., R. V. McGehee, P. U. Rodda, and K. Young. 1972. Geology of the Llano region and Austin area. Univ. Texas Bur. Econ. Geol. Guidebook No. 13, Austin.

Blair, W. F. 1950. The biotic provinces of Texas. Texas J. Sci. 2:94–117.

Brattstrom, B. H. 1963. A preliminary review of the thermal requirements of amphibians. Ecology 44:238–255.

Brune, G. 1975. Major and historical springs of Texas. Texas Water Devel. Board Report 189, Austin.

Correll, D. S., and M. C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, Texas.

Goines, W. H. 1967. Temperatures of Texas streams. Texas Water Devel. Board Report 65, Austin.

Maclay, R. W. 1974. Hydrogeology of the Edwards Limestone Reservoir. Pp. 51–57. *In* P. R. Rose (Ed.), Stratigraphy of Edwards Group and Equivalents, Eastern Edwards Plateau, Texas. South Texas Geol. Soc., San Antonio.

Meinzer, O. E. 1940. Hydrology. McGraw-Hill Book Co., New York.

Mitchell, R. W., and J. R. Reddell. 1971. The invertebrate fauna of Texas caves. Pp. 35–90. *In* E. L. Lundelius and B. H. Slaughter (Eds.), Natural History of Texas Caves. Gulf Natural History Press, Dallas.

Mount, J. R. 1962. Ground-water conditions in the vicinity of Burnet, Texas. Texas Water Devel. Board Memorandum Report 62-01, Austin.

———. 1963. Investigation of ground-water resources near Fredericksburg, Texas. Texas Water Devel. Board Memorandum Report 63-03, Austin.

Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Evol. Biol. 2:321–428.

Rose, P. R. 1972. Edwards Group, surface and subsurface, central Texas. Univ. Texas Bur. Econ. Geol. Report Invest. 74, Austin.

Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42:95–125.

Stricklin, F. L., Jr., C. I. Smith, and F. E. Lozo. 1971. Stratigraphy of Lower Cretaceous Trinity deposits of central Texas. Univ. Texas Bur. Econ. Geol. Report Invest. 71, Austin.

Sweet, S. S. 1976. *Eurycea*: spring and cave salamanders of the Edwards Plateau. Texas Caver 1976:60–62.

———. 1977. Natural metamorphosis in *Eurycea neotenes*, and the generic allocation of the Texas *Eurycea* (Amphibia: Plethodontidae). Herpetologica 33:364–375.

———. 1978. The Evolutionary Development of the Texas *Eurycea*. Ph.D. Dissertation, University of California at Berkeley (Diss. Abst. Intl. No. 7904619).

Texas Water Development Board. 1976. Publications Catalog. Texas Water Devel. Bd., Austin.

United States Geological Survey. 1979. Index to Topographic Maps of Texas, U.S. Geol. Surv., Denver.

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Appendix I

Locality and repository data for 100 populations of *Eurycea neotenes*. Names of springs are capitalized if they appear on USGS topographic maps or are fixed in local usage; otherwise they generally correspond to the nearest named drainage. Elevations are given in feet to facilitate use of existing USGS maps. Latitude and longitude coordinates are the primary locality data, and translate to a circle of 10 m radius in the field. Distances are airline to the center of the nearest town. Abbreviations for museum collections are as follows: AMNH (American Museum of Natural History), CAS (California Academy of Sciences), CU (Cornell University), FMNH (Field Museum of Natural History), MVZ (Museum of Vertebrate Zoology, University of California at Berkeley), SSS (personal collection of author to be deposited at MVZ), TCWC (Texas Cooperative Wildlife Collection, Texas A&M University), TNHC (Texas Natural History Collection, University of Texas at Austin) and USNM (National Museum of Natural History).

Texas. Bandera Co.: Pear Tree Spring, 1600 ft; 29°40′44″ N, 99°11′14″ W; 12.0 km SW Bandera (MVZ 119497–9). Indian Spring, 1600 ft; 29°40′48″ N, 99°11′14″ W; 12.3 km SW Bandera (MVZ 119500–6). Cazey Creek east spring, 1820 ft; 29°44′15″ N, 99°20′20″ W; 11.7 km SW Medina (MVZ 119350–9). Townsend Camp Hollow spring, 1810 ft; 29°44′08″ N, 99°22′07″ W; 12.0 km SW Medina (MVZ 119360–77, 122833–7). Cazey Creek west spring, 1830 ft; 29°43′44″ N, 99°22′13″ W; 13.4 km SW Medina (MVZ 119378–85). Weed Bluff spring, 1910 ft; 29°44′46″ N, 99°25′25″ W; 17.9 km SW Medina (MVZ 119489–96). Sutherland Hollow spring, 1930 ft; 29°44′58″ N, 99°25′40″ W; 17.9 km SW Medina (MVZ 119386–488). Devil's Bathtub Spring, 1940 ft; 29°47′02″ N, 99°26′33″ W; 19.4 km WSW Medina (MVZ 119629). Clement Springs, 1620 ft; 29°42′49″ N, 99°17′22″ W; 7.5 km NW Tarpley (MVZ 119507–601). Hondo Creek tributary spring, 1600 ft; 29°42′24″ N, 99°21′30″ W; 11.2 km NW Tarpley (MVZ 119602). Hondo Creek spring, 1675 ft; 29°43′09″ N, 99°22′12″ W; 11.8 km NW Tarpley (MVZ 119603–10). Seco Creek spring, 1700 ft; 29°42′42″ N, 99°24′58″ W; 15.8 km NW Tarpley (MVZ 119611–28). Mill Creek spring, 1940 ft; 29°47′30″ N, 99°30′10″ W; 7.4 km NE Vanderpool (MVZ 119630–743, TNHC 21673 [41]). Wedgeworth Creek north spring, 1850 ft; 29°48′33″ N, 99°33′55″ W; 7.4 km N Vanderpool (MVZ 119804–935, 122828–40). Wedgeworth Creek south spring, 1820 ft; 29°47′48″N, 99°33′53″ W; 6.7 km N Vanderpool (MVZ 119760–803). Sabinal River headwaters spring, 1840 ft; 29°49′34″ N, 99°34′00″ W; 8.6 km N Vanderpool (TNHC 21676 [5]). BELL CO.: Salado Springs, 570 ft; 30°56′36″ N, 97°32′09″ W; 0.6 km NE Salado (private collection of Bryce C. Brown, Baylor Univ.). BEXAR CO.: Clear Fork Cibolo Creek spring, 960 ft; 29°41′44″ N, 99°23′48″ W; 8.5 km SE Bulverde (MVZ 119954–120026, 122802–12). Cherry Spring and Walnut Spring, 940 ft, 950 ft; 29°40′58″ N, 99°24′00″ W, 29°40′48″ N, 99°23′59″ W; 10.1, 10.6 km SE Bulverde (CAS 7596, 80984, CU 4194 [7], 4427 [12], 4450 [16]). Leon Springs, 1160 ft; 29°39′46″ N, 98°38′12″ W; 1.0 km W Leon Springs (MVZ 120095–101). Helotes Creek spring, 1240 ft; 29°38′15″ N, 98°41′40″ W; 6.7 km N Helotes (FMNH 36845, 91036–8, 91039 [13], 91053, MVZ 120027–94, TNHC T6295–302, 21671 [4], USNM 103161). Culebra Creek spring, 1130 ft; 29°35′05″ N, 98°45′40″ W; 6.4 km WSW Helotes (MVZ 120102–4). BLANCO CO.: Boardhouse Spring, 1300 ft; 30°06′40″ N, 98°18′07″ W; 11.5 km ENE Blanco (MVZ 120105–54). Cove Branch Creek spring, 1240 ft; 30°03′58″ N, 98°20′47″ W; 7.2 km ESE Blanco (MVZ 120156). Blanco River spring, 1300 ft; 30°05′45″ N, 98°25′10″ W; 0.2 km S Blanco (MVZ 120157–66). Zercher Spring, 1340 ft; 30°06′10″ N, 98°27′25″ W; 3.0 km W Blanco (TCWC uncatalogued). COMAL CO.: Bear Creek spring, 1020 ft; 29°48′12″ N, 98°15′17″ W; 7.5 km ESE Smithson Valley (SSS 13617–22). Dry Bear Creek spring, 1060 ft; 29°48′57″ N, 98°14′48″ W; 8.3 km WSW Sattler (MVZ 120270–3). Bailey Ranch spring, 950 ft; 29°53′48″ N, 98°08′12″ W; 7.7 km NE Sattler (MVZ 120255–69). Devil's Backbone spring, 1120 ft; 29°55′50″ N, 98°09′33″ W; 8.6 km N Sattler (AMNH 60790, MVZ 120167–254). Rebecca Creek Spring, 1080 ft; 29°55′57″ N, 98°22′22″ W; 6.2 km NE Spring Branch (MVZ 120274–6, TCWC 44515–22, 44534). Puter (Turkey) Creek spring, 1140 ft; 29°55′57″ N, 98°23′20″ W; 5.6 km NE Spring Branch (MVZ 120277–381). Honey Creek Cave spring, 1100 ft; 29°50′51″ N, 98°29′30″ W; 9.3 km SW Spring Branch (MVZ 120382–3, 120385–8). EDWARDS CO.: Dutch Creek spring, 1860 ft; 29°39′10″ N, 100°06′12″ W; 10.9 km SW Barksdale (MVZ 120598–731, 122815–20). Pulliam Creek spring, 1800 ft; 29°50′04″ N, 100°07′25″ W; 14.7 km NW Barksdale (MVZ 120732–76). Spring Creek spring, 1640 ft; 29°41′28″ N, 100°07′42″ W; 9.8 km WSW Barksdale (MVZ 120777). GILLESPIE CO.: Trough Springs, 1900 ft; 30°08′36″ N, 99°04′13″ W; 12.8 km N Kerrville (MVZ 120778–822). Cottonwood Spring, 2010 ft; 30°10′32″ N, 99°09′58″ W; 12.5 km N Kerrville (TNHC T6303–14). House Spring, 1900 ft; 30°08′11″ N, 99°14′18″ W; 7.7 km N Ingram (MVZ 120874–83, TCWC 44504–8). Fredericksburg (TCWC 14160–3). HAYS CO.: Fern Bank (Little Arkansas) Spring, 800 ft; 29°59′00″ N, 98°00′45″ W; 8.3 km E Wimberley (MVZ 120884–938, TCWC 13104, 13701–9, 14182–3, 17575–7, 18520–6, 26825–30, 33293–4, 34922–9). Spring 1.6 km SE Fern Bank Springs (TCWC 26821–4). Wimberley, beside Blanco River 0.1 km W hwy 32 (A. Hamilton, personal communication, 1973). Cypress Creek spring, 850 ft; 29°59′55″ N, 98°06′03″ W; 0.5 km NNW Wimberley (MVZ 120939–63). KENDALL CO.: East Curry Creek spring, 1240 ft; 29°57′45″ N, 98°32′18″ W; 1.8 km WSW Kendalia (MVZ 121195–205, TCWC 44523–9). Victor Phillip Water Cave spring, 1260 ft; 29°52′57″ N, 98°40′51″ W; 11.0 km NNE Boerne (MVZ 121206–27). Brown's Creek spring, 1400 ft; 29°47′45″ N, 98°44′27″ W; 2.9 km E Boerne (TCWC 44509–14). Balcones Creek spring, 1470 ft; 29°44′18″ N, 98°44′27″ W; 5.1 km SSW Boerne (MVZ 121228). Cibolo Creek tributary spring, 1810 ft; 29°48′30″ N, 98°51′44″ W; 13.1 km WNW Boerne (MVZ 121229–339). Bear Creek spring, 1800 ft; 29°48′15″ N, 98°52′10″ W; 13.3 km WNW Boerne (MVZ 121340–67). KERR CO.: Ayala Spring, 1830 ft; 30°03′26″ N, 99°04′25″ W; 6.4 km ENE Kerrville (MVZ 121396–403). Quinlan Creek tributary spring, 1810 ft; 30°05′11″ N, 99°05′28″ W; 6.9 km NE Kerrville (MVZ 121404). 176 Spring, 1870 ft; 30°05′18″ N, 99°19′14″ W; 2.6 km NNE Hunt (MVZ 121405–66, TCWC CS-108–12). Unnamed creek spring, 1860 ft; 30°01′00″ N, 99°21′06″ W; 6.4 km S Hunt (MVZ 121524–43). Fessenden Branch spring, 1890 ft; 30°09′58″ N, 99°21′03″ W; 2.7 km SE Mountain Home (MVZ 121467–84). Honey Creek spring, 1900 ft; 30°06′02″ N, 99°21′42″ W; 4.5 km NW Hunt (MVZ 121485–6). North Fork Guadalupe River Spring, 1880 ft; 30°03′04″ N, 99°26′54″ W; 11.4 km WSW Hunt (MVZ 121487). Lange Ravine east spring, 1860 ft; 30°01′57″ N, 99°23′05″ W; 6.2 km SW Hunt (MVZ 121488–522). Lange Ravine west spring, 1860 ft; 30°01′57″ N, 99°23′07″ W; 6.4 km SW Hunt (MVZ 121423). Edmunson Creek east spring, 1900 ft; 30°00′23″ N, 99°21′44″ W; 9.3 km

SSW Hunt (MVZ 121544–58). Edmunson Creek west spring, 1880 ft; 30°00′21″ N, 99°21′54″ W; 9.3 km SW Hunt (MVZ 121559–61). Buffalo Creek spring, 1900 ft; 29°58′18″ N, 99°22′35″ W; 10.4 km SW Hunt (MVZ 121562–83). Chimney Spring, 1884 ft; 30°00′19″ N, 99°24′25″ W; 9.9 km SW Hunt (MVZ 121584–94). Cherry Creek spring, 1910 ft; 30°00′34″ N, 99°24′38″ W; 10.1 km SW Hunt (MVZ 121595–617). Fall Creek spring, 1910 ft; 29°54′45″ N, 97°12′20″ W; 15.4 km SSW Kerrville (MVZ 121670–894). Lambs Creek spring, 1900 ft; 29°55′20″ N, 99°14′21″ W; 17.0 km SSW Kerrville (MVZ 121895–2831). Turtle Creek spring, 1980 ft; 29°59′06″ N, 99°15′51″ W; 12.8 km SW Kerrville (MVZ 121618–69). Robinson Creek spring, 1840 ft; 29°54′55″ N, 99°15′08″ W; 13.0 km NNW Medina (MVZ 122078–90). Wallace Creek spring, 1700 ft; 29°54′48″ N, 99°17′52″ W; 13.9 km NNW Medina (MVZ 122091–3). MEDINA CO.: Seco Creek spring, 1310 ft; 29°35′17″ N, 99°23′58″ W; 4.5 km SSE jct Bandera, Medina and Uvalde cos. (MVZ 122125–9). Richter Springs, 1400 ft; 29°35′32″ N, 99°23′07″ W; 15.0 km SE Utopia (MVZ 122094). New Pump Spring, 1580 ft; 29°36′14″ N, 99°21′42″ W; 16.6 km ESE Utopia (MVZ 122095–108). Yellow Spring, 1525 ft; 29°36′56″ N, 99°22′05″ W; 17.1 km E Utopia (MVZ 122109–24) REAL CO.: West Sabinal River tributary spring, 1620 ft; 29°41′13″ N, 99°37′22″ W; 12.2 km NW Utopia (TNHC 21669 [17], 21670). Harris Spring, 1640 ft; 29°43′24″ N, 99°37′10″ W; 14.7 km NW Utopia (TNHC 21674 [40]). Ash Hollow spring, 1840 ft; 29°44′07″ N, 99°38′37″ W; 13.4 km ENE Leakey (MVZ 122142–364). Mud Spring, 1910 ft; 29°40′30″ N, 99°40′02″ W; 8.0 km NE Rio Frio (MVZ 122377–98). Little Dry Frio Creek tributary spring, 1800 ft; 29°43′12″ N, 99°40′10″ W; 11.2 km E Leakey (MVZ 122365–76). South Prong Cypress Creek north spring, 1830 ft; 29°47′58″ N, 99°38′54″ W; 14.9 km NE Leakey (MVZ 122399–407). South Prong Cypress Creek south spring, 1910 ft; 29°47′46″ N, 99°39′58″ W; 14.7 km NE Leakey (MVZ 122408–76, 122832, TCWC CS-149–50). East Frio River spring, 1850 ft; 29°51′02″ N, 99°40′02″ W; 18.6 km NE Leakey (MVZ 122477–587). Bee Cave Hollow spring 2030 ft; 29°54′25″ N, 99°47′27″ W; 17.6 km N Leakey (MVZ 122592–671). Short Prong Frio River spring, 2000 ft; 29°55′00″ N, 99°47′30″ W; 19.2 km N Leakey (MVZ 122588–91). Prade Ranch spring, 1950 ft; 29°54′51″ N, 99°47′02″ W; 19.2 km N Leakey (FMNH 55086 [2], 55087–90, 55092–3, 55095–6). Old Faithful Spring, 1460 ft; 29°40′48″ N, 100°00′51″ W; 0.8 km N Camp Wood (MVZ 122672). Mullen Hollow spring, 1940 ft; 29°57′57″ N, 99°57′52″ W; 14.4 km NNE Barksdale (MVZ 122673–86). TRAVIS CO.: Stillhouse Hollow spring, 780 ft; 30°22′20″ N, 97°45′45″ W; 11.0 km NNW Austin (MVZ 122695–703). McDonald Well spring, 770 ft; 30°26′57″ N, 97°51′12″ W; 5.0 km NNW Four Points (Hickmuntown) (MVZ 122705–11, TCWC 44530–2). Spring near Marshall Ford Dam (Mansfield Dam) (Baker, 1961). Jack Dies Ranch spring near Dodd City (TNHC 21640–3). UVALDE CO.: Onion Creek spring, 1500 ft; 29°34′57″ N, 99°34′51″ W; 6.2 km SW Utopia (MVZ 122764–7). Salt Marsh Creek spring, 1800 ft; 29°37′03″ N, 99°36′06″ W; 6.7 km W Utopia (MVZ 122727–63). Bludworth Ranch spring, 1500 ft; 29°31′40″ N, 99°39′12″ W; 17.0 km SW Utopia (MVZ 122768–74). Spring on bank of Frio River, about 3.2 km S Garner State Park (TCWC 2114–9). Montell Springs, Montell (TNHC 21658–9). Montell Creek spring, 1530 ft; 29°43′28″ N, 100°04′48″ W; 8.3 km NW Montell (MVZ 122775). VAL VERDE CO.: San Felipe Springs, 910 ft; 29°22′22″ N, 100°53′09″ W; 1.4 km ENE Del Rio (MVZ 122791–2). WILLIAMSON CO.: San Gabriel River spring, 660 ft; 30°39′15″ N, 97°40′01″ W; 2.1 km NNE Georgetown (MVZ 122801). Krienke Spring, 800 ft; 30°30′22″ N, 97°44′54″ W; 5.1 km NW Round Rock (TNHC T1802–16, T6334–9, 31013 [42]). Spring 2.4 km NE Round Rock, Brushy Creek (TNHC 6242).

APPENDIX II

Elevation and abbreviated locality data for 55 springs not inhabited by *Eurycea neotenes*. Format as in Appendix I.

TEXAS. BANDERA CO.: Kindla Spring, 1260 ft; 29°44′54″ N, 99°06′54″ W. Elm Creek spring, 1680 ft; 29°46′06″ N, 99°17′18″ W. North Prong Medina River spring, 1650 ft; 29°51′25″ N, 99°21′45″ W. BELL CO.: Salado Springs, 560 ft; 30°56′23″ N, 97°32′06″ W. BEXAR CO.: San Antonio Springs, 680 ft; 29°27′56″ N, 98°28′06″ W. BLANCO CO.: 290 × 286 spring, 1280 ft; 30°12′32″ N, 98°22′28″ W. Crabapple Creek spring, 1380 ft; 30°06′08″ N, 98°30′35″ W. COMAL CO.: Frio Spring, 1100 ft; 29°55′55″ N, 98°10′46″ W. Lonesome Valley Spring, 1060 ft; 29°56′00″ N, 98°10′21″ W. KENDALL CO.: Simmons Creek spring, 1080 ft; 29°54′53″ N, 98°29′57″ W. Little Water Cave spring, 1100 ft; 29°53′16″ N, 98°31′10″ W. Alzafar Creek spring, 1280 ft; 29°53′00″ N, 98°39′19″ W. Swede Creek spring, 1180 ft; 29°52′02″ N, 98°34′38″ W. Panther Creek spring, 1100 ft; 29°52′18″ N, 98°32′42″ W. Fourlevel Water Cave spring, 1100 ft; 29°52′41″ N, 98°31′33″ W. KERR CO.: Hasenwinkle Creek spring, 1800 ft; 30°04′14″ N, 98°57′40″ W. Cross Creek Ranch spring, 1850 ft; 30°06′57″ N, 98°57′40″ W. East Town Creek spring, 1820 ft; 30°05′58″ N, 99°07′31″ W. Lange Box Spring, 2000 ft; 30°02′05″ N, 99°23′45″ W. Guadalupe River headwaters spring, 1920 ft; 30°03′10″ N, 99°29′42″ W. Bee Caves Creek lower spring, 1900 ft; 30°03′30″ N, 99″27′33″ W. Bee Caves Creek upper spring, 1940 ft; 30°02′13″ N, 99°25′21″ W. Johnson Creek spring, 1900 ft; 30°10′46″ N, 99°22′45″ W. Honey Creek Ranch spring, 1900 ft; 30°06′12″ N, 99°22′07″ W. EDWARDS CO.: Pulliam Creek lower spring, 1800 ft; 29°50′22″ N, 100°07′19″ W. Pulliam Creek upper spring, 1820 ft; 29°51′02″ N, 100°07′45″ W. GILLESPIE CO.: Spring Creek spring, 2010 ft; 30°20′35″ N, 99°04′48″ W. Live Oak Creek spring, 2020 ft; 30°21′08″ N, 99°01′26″ W. Pecan Creek spring, 2000 ft; 30°22′03″ N, 98°58′22″ W. Willow Creek spring, 1900 ft; 30°21′51″ N, 98°45′48″ W. HAYS CO.: Smith Creek lower spring, 1080 ft;

30°01′02″ N, 98°04′27″ W. Smith Creek upper spring, 1100 ft; 30°01′35″ N, 98°04′45″ W. Ben McCulloch Spring, 940 ft; 30°07′40″ N, 98°00′45″ W. Blanco River spring, 820 ft; 29°59′32″ N, 98°05′30″ W. Spring 2.4 km E Payton, 1270 ft; 30°06′33″ N, 98°16′08″ W. Rancho Cima Dam spring, 1040 ft; 29°56′23″ N, 98°09′06″ W. Spring 1.6 km SE Signal Hill, 880 ft; 30°10′48″ N, 97°56′07″ W. KINNEY CO.: Las Moras Springs, 1100 ft; 29°18′32″ N, 100°25′16″ W. REAL CO.: Deer Creek spring, 1620 ft; 29°39′27″ N, 99°40′03″ W. Eagle Cliff spring, 1880 ft; 29°57′38″ N, 99°57′12″ W. TRAVIS CO.: Sheep Hollow spring, 980 ft; 30°35′08″ N, 97°58′07″ W. Spicewood Springs, 730 ft; 30°21′55″ N, 97°44′59″ W. Canyon Spring, 1020 ft; 30°15′35″ N, 97°53′03″ W. Short Spring Branch spring, 850 ft; 30°15′00″ N, 97°53′18″ W. UVALDE CO.: Bear Creek lower spring, 1700 ft; 29°36′18″ N, 99°36′50″ W. Bear Creek upper spring, 1740 ft; 29°36′39″ N, 99°36′30″ W. Cowan Springs, 1260 ft; 29°30′17″ N, 99°42′27″ W. Cold Springs Ranch Spring, 1410 ft; 29°36′45″ N, 99°44′25″ W. Concan Springs, 1220 ft; 29°29′47″ N, 99°42′40″ W. WILLIAMSON CO.: Andice spring, 970 ft; 30°46′58″ N, 97°50′16″ W. Sycamore Springs, 990 ft; 30°48′48″ N, 97°55′33″ W. South Fork San Gabriel spring, 850 ft; 30°37′06″ N, 97°50′40″ W. Jim Hogg Road spring, 830 ft; 30°40′31″ N, 97°45′38″ W. Crockett Gardens Springs, 810 ft; 30°39′50″ N, 97°45′05″ W. Sideriver spring, 760 ft; 30°36′00″ N, 97°45′00″ W.

APPENDIX III

Numbers of springs marked on US Geological Survey 7½′ topographic maps within the area outlined on Fig. 1A. Italicized entries lie within the known range of *Eurycea neotenes*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
A																												0	5	0	0	0	0	2	0
B																										4	0	0	2	0	0	0	0	1	0
C																								2	0	15	0	6	1	0	0	0	0	0	0
D																						1	3	0	0	8	1	0	0	0	0	2	*0*	2	0
E																				2	1	1	0	0	0	0	7	0	0	1	1	2	0	0	1
F	0	0	0	0	0	0	0	0	0	0	0	0	0	3	4	11	0	0	1	8	9	3	0	0	0	5	1	0	0	*2*	*12*	*0*	0	0	1
G	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	2	0	6	3	1	1	6	1	0	2	3	1	*10*	*8*	*0*	0	0	0
H	0	0	0	0	0	0	0	0	0	0	0	0	1	—	0	—	—	—	—	6	4	7	21	14	5	0	0	1	0	*0*	*1*	*0*	0	0	0
I	0	0	0	0	0	0	0	0	0	0	0	0	0	1	—	—	—	—	—	9	7	*12*	*16*	*0*	0	0	0	0	1	*2*	*0*	*0*	0	0	0
J	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	*2*	*3*	*1*	*3*	*0*	*0*	*0*	*0*	*6*	*6*	*2*	*2*	*1*	*0*	0	0	0	0
K	1	0	0	0	0	3	0	0	0	0	0	0	*8*	0	0	0	*1*	*21*	*13*	*4*	*23*	*26*	*10*	*6*	*2*	*0*	*8*	*5*	*5*	*0*	*0*	0	0	0	0
L	0	0	0	0	0	1	0	0	0	*2*	*1*	*1*	*7*	*31*	*13*	*7*	*0*	*9*	*14*	*8*	*0*	*3*	*0*	*2*	*2*	*3*	*2*	*0*	*0*	*0*	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	*1*	*0*	*1*	*34*	*43*	*12*	*4*	*4*	*25*	*12*	*5*	*1*	*12*	*3*	*3*	*6*	*2*	*1*	*2*	*0*	0	0	0	0	0	0
N		0	1	0	0	0	0	0	0	0	2	*1*	*10*	*33*	*9*	*43*	*8*	*14*	*37*	*14*	*10*	*8*	*15*	*11*	*0*	*11*	*0*	*0*	0	0	0	0	0	0	0
O			0	0	0	0	0	0	0	0	0	*5*	*12*	*15*	*9*	*2*	*14*	*3*	*15*	*3*	*9*	*0*	*8*	*3*	*0*	*0*	0	0	0	0	0	1	0		
P				0	1	1	*1*	0	2	0	0	*1*	*0*	*4*	*0*	*0*	*1*	0	0	0	0	0	0	0	0	0	0	0	0	1	0				
Q						3	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2						
R							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								

APPENDIX IV

Mean probabilities of habitation by *Eurycea neotenes* (see text) for springs marked on US Geological Survey 7½′ topographic maps within the area outlined on Fig. 1A. Italicized entries lie within the known range of *Eurycea neotenes*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
A																												0	37	0	0	0	0	31	0
B																										52	0	0	41	0	0	0	0	34	0
C																								35	0	58	0	37	37	0	0	0	0	0	0
D																						46	29	0	0	64	53	0	0	0	0	39	*0*	29	0
E																				56	43	58	0	0	0	0	65	0	0	37	29	44	0	0	18
F	0	0	0	0	0	0	0	0	0	0	0	0	0	51	48	51	0	0	67	43	29	37	0	0	0	75	62	0	0	*34*	*53*	*0*	0	0	11
G	0	0	0	0	0	0	0	0	0	0	0	51	53	0	0	0	0	29	0	59	53	51	58	64	62	0	34	67	67	*61*	*48*	*0*	0	0	0
H	0	0	0	0	0	0	0	0	0	0	0	0	59	—	0	—	—	—	—	53	54	48	59	78	62	0	0	37	0	*0*	*37*	*0*	0	0	0
I	0	0	0	0	0	0	0	0	0	0	0	0	0	64	—	—	—	—	—	53	53	*46*	*48*	*0*	0	0	0	0	18	*41*	*0*	*0*	0	0	0
J	0	0	0	0	0	0	0	0	0	0	0	0	68	57	0	0	0	*51*	*54*	*46*	*54*	*0*	*0*	*0*	*0*	*58*	*56*	*47*	*53*	59	*0*	0	0	0	0
K	81	0	0	0	0	71	0	0	0	0	0	0	*73*	0	0	0	*59*	*61*	*58*	*61*	*64*	*53*	*48*	*56*	*53*	*0*	*46*	*53*	*48*	*0*	*0*	0	0	0	0
L	0	0	0	0	0	84	0	0	0	*58*	*65*	*84*	*82*	*72*	*70*	*65*	*0*	*62*	*62*	*63*	*0*	*66*	*0*	*61*	*53*	*53*	*48*	*0*	*0*	*0*	0	0	0	0	0
M	0	0	0	0	0	0	0	0	0	*72*	*0*	*81*	*78*	*75*	*83*	*72*	*72*	*66*	*81*	*78*	*48*	*56*	*58*	*61*	*53*	*53*	*65*	*65*	*0*	0	0	0	0	0	0
N		0	48	0	0	0	0	0	0	0	*73*	*62*	*68*	*83*	*79*	*81*	*82*	*80*	*77*	*74*	*56*	*67*	*72*	*70*	*0*	*68*	*0*	*0*	0	0	0	0	0	0	0
O			0	0	0	0	0	0	0	0	0	*70*	*62*	*78*	*75*	*61*	*73*	*86*	*86*	*77*	*72*	*0*	*67*	*64*	*0*	*0*	0	0	0	0	0	29	0		
P				0	29	29	29	0	34	0	0	*65*	*0*	*84*	*0*	*0*	*73*	0	0	0	0	0	0	0	0	0	0	0	0	18	0				
Q						37	24	29	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14						
R							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								