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The Ecology of the Tropical Salamander, Bolitoglossa subpalmata, in Costa Rica

by

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INTRODUCTION

BACKGROUND AND SCOPE OF WORK

Modern ecological concepts have been established and refined mostly from data obtained in north temperate zone studies. Despite the fact that about one-third of the land mass of the earth and nearly two-thirds of its biota occur in the tropic zone, little is known about basic biological processes or ecological relationships under the influence of the tropical sun. The tropical environment is distinguishable from that of extratropical latitudes on the basis of photoperiodicity, temperature, heat budget, and productivity; a combination of factors which produces a unique ecologic setting.

Although numerous works have dealt with the tropics, invariably the definition of the region has been inadequate from an ecological point of view. In order to evaluate the characteristics of tropical and temperate regions it is necessary to present a foundation of common understanding on the nature of the tropical environment.

The tropics are usually defined as the warm latitudes lying between 23° 27' N and S of the equator. Because of the sun's relation to the earth this latitudinal region receives maximum solar radiation. If the earth's surface were of uniform composition and physiography, it might be expected that a characteristic environment inhabited by a tropical biota would be found throughout the region. The nonuniform distribution of land and water and physiographic diversity of land masses modify distribution of the heat budget so that irregularities occur. On the basis of known limits of distribution of tropical biotas it has been suggested that the tropical environment in its broadest sense is limited on the north and south

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in terrestrial and fresh water situations by the 24° C mean annual isotherms, corrected to sea level. Tropical marine habitats occur in areas where the mean surface temperature in the coldest month is greater than 21° C. The tropical region is here defined as a thermal zone occurring in extremes to 35° N Lat. and about 32° S Lat. Variations in north and south extent of the tropic boundary are due to size and elevation of the included land areas, and effects of oceanic currents.

Within this region the daylight period is never less than 10 hours in 24, nor more than 14. Farther north and south the photoperiod may range from zero to 24 hours depending upon the season. Solar radiation in the tropic belt averages 860 gm cal/cm^2/day (range 720 to 1,000), whereas in extratropical areas the average is 600 gm cal/cm^2/day (range 0 to 1,200) (Coen, pers. comm.). On a heat budget basis the tropics receive the greatest proportion of solar energy and the energy is evenly distributed over the year.

Lack of seasonality is sometimes regarded as a tropical character, but actually the seasons are obscured because diel extremes of temperature and humidity show greater range of variation than annual climatic cycles. Seasonal changes in the tropics are expressed principally by differences in rainfall distribution.

In a general way there is a correspondence of biota with the delimiting thermal boundaries, although broad areas of transition may be present. High montane and alpine regions dissect much of the tropics. Within the 24° C (sea level) isotherm these regions are tropical in that they are exposed to the same light periodicity and energy magnitudes as the lowlands, although their climatic parameters may at first sight correspond to those of extratropical localities.

Extratropical plethodontid salamanders have been one of the most widely studied groups of amphibians. The great diversity within the family and its broad distribution offer excellent opportunities for studies of comparative ecology, as have been demonstrated by DUNN (22), GROBMAN (32), HAIRSTON (33), and ORGAN (56). Although the Plethodontidae is the only family of salamanders found in the tropics, no intensive study of any tropical representative has been previously attempted. Probably few other species of salamanders are so suited for sustained field investigations as is *Bolitoglossa subpalmata* (Boulenger). Although practically nothing was known of its life history, the species' remarkable abundance on the Cerro de la Muerte of Costa Rica indicated an almost ideal situation for continuous study throughout its vertical range of distribution, accessible by the Inter-American Highway (Fig. 1).

The objectives of the present study are fivefold: (1) to determine the local distribution, habitat selection, and life history of *B. subpalmata;* (2) to evaluate the significance of populational characters as expressed by the ecology of the species; (3) to provide an understanding of the basic biology of salamanders in the tropics, with particular emphasis on ecologic differences that may exist between populations in tropic and temperate zones; (4) to determine the feasibility of applying ecologic and demographic methods to tropical organisms; and (5) to develop a foundation for future work in tropical population ecology.

Preliminary field work was carried out in June of 1961. Fulltime study was begun in August, 1961, and continued until September of 1962. Subsequent visits to the study area were made as late as October, 1963. Approximately 160 man-days were devoted to field work during the first 15 months and nearly 12,000 miles were traveled in Costa Rica in direct relation to the study. Information was gathered on over 4,000 specimens of *B. subpalmata.* More than 3,000 were preserved and catalogued. Almost 1,000 others were marked and studied in the field throughout the year, while another 300 were used in activity studies and laboratory procedures.

METHODS

To evaluate local climatic conditions, measurements were taken weekly from September 15, 1961, to September 15, 1962, at six standard weather stations established at 305 m (1,000 ft.) intervals of elevation on the northwest and south facing slopes of the Cerro de la Muerte in Costa Rica. Because of the possibility of theft or tampering, all stations were placed on local fincas. As a result of this precaution, the station at Finca Chávez was 37 m (120 ft). below the standard interval. The locations are shown in Fig. 2. Temperature records from three stations could not be obtained for a period of two weeks in September, 1961. At San Cristóbal the rain gauge was tampered with on two occasions.

Measurements from weather stations were obtained by use of Taylor maximum-minimum thermometers, each calibrated with standards at the Servicio Meteorológico de Costa Rica. All readings were converted to Centigrade. Rain gauges were especially constructed and also calibrated by this agency. Readings of precipitation were made directly with a graduated cylinder.

Field elevations were measured with a Thommen altimeter reading to 25 ft. intervals, and converted to the nearest meter. Because of rapid fluctuations in atmospheric pressure, the given elevations represent an average of at least six readings for each locality within the study area. Before and after each daily trip the instrument was calibrated at a known bench mark elevation. Topographic sheets of the Cerro de la Muerte were not available during the period of field study; however, quadrangles for the northern part of the region have been published subsequently by the Instituto Geográfico de Costa Rica in cooperation with the Inter-American Geodetic Survey. Elevations and place names given by these maps are included in Fig. 2. The maximum variance between field readings and aerial planimetry was less than 50 m.

Relative humidity measurements were taken with a Bachrach (Model SAC) sling psychrometer at the beginning and end of a study period at each locality. When random collecting was done for less than a half-hour, only a single reading was taken.

Except for weather station records, all temperatures were measured with a Schultheis rapid stabilizing thermometer. Temperature readings of soil, air (at 2 cm, 15 cm, ± 150 cm), and beneath rocks or debris (microhabitat) were obtained at the start and completion of every study period of more than one-half hour at the same site.

At three month intervals 15 quadrats of 186 sq. m (2,000 sq. ft.) were taken; one at each 152 m (500 ft.) of vertical interval from elevations of 2,134 m (7,000 ft.) on both the NW and S slopes of the Cerro. This area was estimated to offer optimal results after several preliminary trials. Collecting procedures within quadrats were consistent; all surface litter was cleared and removed, but no digging was done. Habitat, size, and sex were noted for all specimens. Areas were not re-sampled except for immigration studies. Efforts were made to collect from similar environmental situations; *i.e,* topography, slope, and vegetation, in each site.

At other times areas of various dimensions were sampled to supplement observations on relative densities, activity cycles, and local distribution. Nearly 2,500 individuals were collected for this part of the study.

Six salamander populations were marked between elevations of 2,286 m (7,500 ft) and 3,200 m (10,500 ft.). Their locations are shown in Fig. 2. Each was studied at monthy intervals for a year. Limits of elevation for this phase were determined by the available densities of *B. subpalmata* and feasibility of study without serious disturbance of habitat. The lowest of the six (2,286 m. on the NW slope) was experimental in that it consisted of 30 marked and released individuals taken from higher elevations (Population Ix).

The five remaining sites were located at approximately 305 m (1,000 ft.) vertical intervals. Three were located on the NW slope and two on the southern incline. Population IV, at 2,560 m. (8,400 ft.), consisted of a total of 46 individuals captured and marked during the year. Population III, located at 2,926 m (9,600 ft.), included 302 marked animals; 407 salamanders were marked in Population II near the summit at 3,200 m (10,500 ft.) and was the highest study site established. On the southern slope, at an elevation of 2,926 m, Populations I and IA were set up; the latter after destruction of much of the habitat of Nº I by road building. Subsequently, Nº I was studied only in respect to individuals previously marked. These two samples included 80 and 101 animals, respectively.

The marking period of Population II was from August, 1961, through July of 1962. Numbers III and IV were studied from September, 1961, to August, 1962. The site of Population I was destroyed in November, 1961, and at that time an alternate site, Nº IA, was established and studied until August, 1962. At the experimental site (Ix) marked specimens were released in August, 1961, and the area was examined at two month intervals. After October of that year, no animals were recovered.

At each study site a stake grid was set up, usually at intervals of about 15 m (50 ft.) providing fixed references for azimuths and measurements. To the extent that it could be accomplished with minimum disturbance of the habitat, all surface cover was removed and replaced. Objects that could not be moved without permanent disturbance or destruction were left in place. Every available specimen within the area was marked by toe clipping, measured for snout-vent length, and sexed. Notes were taken on breeding condition, and other pertinent characters.

The animals were then returned to the spot at which they were taken. Although marking of new individuals was performed only within a defined area, the surrounding 30 m (100 ft.) zone was examined in the same manner for marked salamanders. All recaptured animals were studied as above. In these sites, 966 individuals were marked and studied during the year.

The study areas varied from 652 sq. m (7,020 sq. ft.) to 1,104 sq. m (11,875 sq. ft.). The size of each area was determined primarily by the number of animals that could be processed in a single day, thus avoiding any nocturnal population shifts.

Measurements of distances were made with a 30 m (100 ft.) Lufkin steel tape. Azimuth readings to the nearest degree were taken with a United States Army Lensatic compass. Care was practiced to avoid any magnetic attraction by extraneous objects.

Nocturnal activity of *B. subpalmata* was studied on six different occasions on the Cerro de la Muerte, between 2,560 m (8,400 ft.) and the summit. Predusk to post-dawn observations were made at five localities which included the marked populations. In each study the site was checked, using a battery headlamp, at two hour intervals throughout the night. A consistent path of examination of the area was followed and equal time allotted to each visit. Following the method of HAIRSTON (33), a salamander was considered 100% active if it had completely emerged from cover and was found in the open, or 50% active if but partially exposed. To avoid negative responses by active animals, none were touched or disturbed. On the night of May 12, 1962, at 2,926 m (9,600 ft.) on the southern slope, all active specimens were collected at each visit. After sunrise the area was thoroughly examined and all available salamanders were collected.

At the beginning and end of each visit, relative humidity and temperatures of the microhabitat, soil and air were recorded.

Each month, samples of *B. subpalmata* were randomly taken at altitudinal intervals of about 150 m (500 ft.); quadrat sites and marked populations were avoided. All specimens were noted as to standard length, number and size of testicular lobes or number and sizes of ova, as well as the condition of secondary sex characters. From each sample paraffin sections were made from individuals selected at 5 mm size intervals to determine the relationship of size and sexual development. Gonads from 250 salamanders were fixed in Carnoy solution, stained with hematoxylin-eosin and sectioned at 8 to 10 micra.

Eggs and attending adults observed in the field were examined at intervals and records taken on egg sizes and stages of development. Thirteen egg clutches with the attending adults were brought to the laboratory and maintained at conditions approximating those of the natural habitat in order to permit study of brooding behavior and development. Information was obtained from a total of 31 clutches and attending adults.

To observe courtship and breeding behavior, males and females were kept together in captivity. The animals were replaced at bi-weekly intervals to ensure optimal physiological conditions. Twenty-four experimental animals were subcutaneously implanted with pituitary glands from fresh *Rana pipiens* and *B. subpalmata* to stimulate breeding and oviposition.

Laboratory experiments were conducted on temperature tolerances and water requirements of *B. subpalmata* as well as on dehydration and rehydration rates. Canned soil samples were taken in the field during most periods of study of the marked populations, quadrats, and activity cycles; classified as to texture and color; then weighed before and after heating at 105⁰ C for 48 hours. Soil moisture values are expressed as percentage of dry weight.

All measurements of specimens are in millimeters. Unless otherwise stated, sizes of individuals are given as standard length (snout to posterior margin of vent). Measurements on living specimens were made by using a grooved board about 30 cm in length wrapped in absorbent paper toweling. The live animal was placed in the groove, dorsal side down, and a millimeter rule placed gently, but firmly, over the ventral surface. Reading were taken to the nearest 0.5 mm. Repeated measurements of the same animals indicated an accuracy of measurement to ± 1.0 mm in adults. Sacrificed animals were killed in hydrous chlorobutanol (Chloretone) and measured with a Helios dial caliper to the nearest 0.1 mm before preservation. Repeated measurements indicated an accuracy of ± 0.2 mm.

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THE ENVIRONMENT

LOCATION AND PHYSIOGRAPHY

The Cordillera de Talamanca dominates the topography of southern Costa Rica. At the northern margin of this range lies the Cerro de la Muerte (9° 35' N Lat., 83° 45' W Long.), one of the larger massifs, rising to an elevation of 3,491 m (11,450 ft.) and surrounded by several satellite peaks of similar heights. It is through and over this region that the Inter-American Highway makes a sinuous vertical transect reaching its highest level at 3,247 m (10,649 ft.). The study region (Fig. 1) included a part of this highway transect some 64 km in length and was limited to elevations above 2,134 m on either side of the summit. Altitudinal limits were established after determining the vertical distribution of *B. subpalmata* and were at least 150 m below levels where this salamander was locally found. The vertical range from the lowest level in the study area to the summit is about 1,100 m.

Extending in a NW-SE direction for over 175 km, the Cordillera de Talamanca includes several peaks of nearly 4,000 m forming a rather uniform anticline in which the southwestern (Pacific) side is more abrupt than the northeastern (Atlantic). Primarily granitic, it has been interrupted by local volcanic activity and complex orogenic processes during the period of emergence which dates from early Miocene (LLOYD, 51; WEYL, 79, 80). The Cerro de la Muerte is the highest region in the cordillera accessible by road. In recent years the actual peak has been renamed Cerro Buena Vista, though the massif itself is still referred to by the earlier name.

Soils on the upper slopes of the cordillera are poorly developed. True soil horizons are usually less than a meter in depth. Frequently a thin humus layer lies in contact with the slightly weathered rock mantle. Due to the complex geologic structure, soil textures and colors are variable. At elevations to approximately 2,135 m, gray-brown sandy and loamy soils predominate although black loam and clay occur in limited areas. Clayey soils, usually yellow-gray, are common between 2,440 and 2,745 m. At higher elevations a gray-brown gravelly loam is typical, although in sheltered areas and depressions deposits of black silty loam occur; the result of localized decomposition of vegetation. WEBER (78) reports pH values of 3.9 to 4.0 for soil samples from Jaboncillo Peak.

CLIMATE AND WEATHER

The narrowness of the isthmus at this latitude (10° N), which separates the Pacific Ocean and Caribbean Sea by less than 120 km, provides Costa Rica with an insular climate lacking any significant continental influence. Within the general pattern of the tropical climate, however, many local factors such as topography, air currents and storm tracks create striking disparities.

Records for precipitation during the first year of the study period are presented in Table I. The lowest annual precipitation, 2,117 mm, was observed at El Empalme (2,134 m). On two occasions the rain gauge was tampered with at Finca San Cristóbal (Hermanos Camacho); however, the annual total of 2,429 mm recorded for this locality is reasonably accurate. At Finca Chávez (2,706 m) 3,142 mm fell, the most recorded. Although no region of the Cerro receives less than 2,000 mm of rainfall per year, there is a distinct dry period from January through March. Following the wettest months, May and June, a short dry period, or Veranillo de San Juan, usually occurs in late July and early August.

Temperature records obtained from six weather stations are given as mean monthly minima and maxima in Table 2. The lowest mean monthly minimum was 0° C, obtained for January and February at Finca Chávez (2,706 m). The highest mean monthly minimum of 10° C at the El Empalme station (2,134 m) occurred from May through November, and at La Cueva del Tigre (2,438 m) on the southern slope in May and July. Average mean minima and maxima for the complete 12 months period ranged from 3.3 to 9.2° C and from 18.1 to 24.1° C. The overriding influence of local conditions is easily seen. Finca Chávez, for example, averages a minimum temperature equal to that of La Georgina, over 300 m higher. Combined weekly rainfall and temperature records (maxima and minima) for El Empalme and La Georgina are shown in Figures 3 and 4.

At 10° N Lat. the period of daylight at the solstice extremes is from 11.5 to 12.5 hours. The sun's zenith lies to the north for four months of the year. Notwithstanding this slight seasonal variation in photoperiod, south-facing montane slopes exhibit markedly higher maximum temperatures because of more extended direct exposure to solar insolation.

Probably the most effective use of temperature records obtained from the weather stations can be made by application of the mean annual biotic temperature of HOLDRIDGE (39, 42). His concept of biotemperature assumes that plants exhibit a consistent dormant response to temperatures of 0° C or lower. Only positive averages are utilized in the computation. Specific values are derived from the formula $B = \frac{\sum \text{mean monthly temperatures} > 0^{\circ}\text{C}}{12}$. Biotemperatures are treated by HOLDRIDGE (39, *et seq.)* as a principal character in his classification of the world vegetation formations on a climatic basis. Altitudinal lapse rates of computed biotemperatures on the Cerro are shown in Fig. 5. The average change of biotemperature with elevation on the northwest slope is approximately 1.6° C for each 300 m interval, while on the more abrupt southern slope it is 3.1° C per 300 m. The biotemperature value at the height of the study area (3,246 m) is estimated by extrapolation as 8.6° C. Measurements of lapse rates taken during several daily observations on the Cerro approximate these values.

Daily atmospheric changes follow a strikingly consistent pattern on the Cerro. Usually the sun will rise on a clear sky, with only isolated puffs of low cumulus clouds visible. As insolation becomes more intense, strong convectional currents develop and by mid-morning the sky is densely overcast. During the dry periods, cloud development may be delayed to mid-afternoon and rain, if any, is slight. For almost ten months of the year visibility becomes reduced to a few meters

TABLE 1

Precipitation in monthly totals at six weather stations on the Cerro de la Muerte. Records were accumulated at weekly intervals from September 15, 1961, to the same date of 1962. Elevation and locations are shown in Fig. 2.

Month	2,134 m El Empalme	2,438 m San Cristóbal	2,706 m Chávez	3,048 m La Georgina	2,743 m La Siberia	2,438 m La Cueva
Jan.	68	45	148	32	20	2
Feb.	10	2	23	18	5	7
Mar.	6	2	27	0	3	3
Apr.	85	69	159	170	157	167
May	210	245	405	416	382	503
June	419	604?	394	382	394	482
July	218	259	312	207	180	196
Aug.	200	203	340	421	314	283
Sept.	261	233+	366	330	334	325
Oct.	248	343	392	402	341	266
Nov.	271	270	325	342	333	417
Dec.	121	154	251	165	146	147
Totals mm.ppt./yr.	2,117	2,429±	3,142	2,885	2,609	2,798

TABLE 2

Temperature records of monthly minima and maxima at six weather stations on the Cerro la Muerte obtained from September 15, 1961, to the same date of 1962. Elevations and locations are shown in Fig. 2. Biotemperatures are discussed in text.
LMWF= Lower Montane Wet Forest; MRF= Montane Rain Forest.

	Elevation and Location											
	2,134 m		2,438 m		2,706 m		3,048 m		2,743 m		2,438 m	
Month	El Empalme		San Cristóbal		Chávez		La Georgina		La Siberia		La Cueva	
	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.
Jan.	7	19	6	16	0	18	1	19	4	20	8	26
Feb.	7	20	6	19	0	19	2	20	4	18	8	25
Mar.	8	22	7	21	1	21	3	22	6	23	8	25
Apr.	9	21	7	18	2	18	3	21	5	22	9	24
May	10	21	8	19	5	19	6	20	6	21	10	22
June	10	20	9	18	6	19	5	20	7	20	9	23
July	10	20	8	17	6	18	2	18	8	21	10	23
Aug.	10	20	5	17	5	19	4	21	7	22	9	24
Sept.	10	20	7	19	3±	20	4	19	6	21	8±	29
Oct.	10	20	9	18	4	18	4	18	7	20	9	23
Nov.	10	19	8	17	5	16	4	18	6	20	9	22
Dec.	9	18	7	18	3	17	3	18	4	21	9	23
Ave.	9.2	20.0	7.2	18.1	3.3	18.5	3.4	19.5	5.8	20.8	8.8	24.1
Biotemp.	14.6		12.6		10.9		11.4		13.3		16.2	
Vegetation Formation	LMWF		LMWF		MRF		MRF		LMWF		LMWF	

soon after noon, followed by heavy but sporadic rains. In late afternoon some thermal stability is reached and the clouds fragment. Visibility alternates from zero to several hundred meters as winds move the clouds over mountain ridges. Darkness is followed by spotty cloud cover but during the night there is gradual clearing of the sky, a reduction of humidity and decrease in temperature.

VEGETATION

The area includes two major climatic vegetation formations: the Tropical Lower Montane Wet Forest and the Tropical Montane Rain Forest (HOLDRIDGE, 40, 41). In this part of the cordillera they have upper limits at 2,500 m and 3,100 m, respectively. Above the latter elevations occurs a poorly defined disclimax community, the páramo, resulting from the invasion of the burned over summit region by elements of a subalpine wet woodland. It is not, however, a climatic formation, as the temperature and precipitation are characteristic of the Montane Rain Forest. Biotemperatures and vegetational formations associated with local climatic patterns are included in Table 2.

Each formation is characterized by certain plant species which reflect some degree of dominance and restriction in distribution. Nomenclature and species determination is based upon information from HOLDRIDGE (40), STANDLEY (68), and WEBER (78).

On the Cerro de la Muerte dominant tree species of the Lower Montane Wet Forest include *Cornus disciflora, Cedrela Tonduzii, Alnus jorullensis, Magnolia poasana, Drimys granadensis* and *Persea Schiedeana.* Several species each of *Miconia, Conostegia* and *Piper* are abundant in the woody undergrowth. On poor soils *Quercus copeyensis* or *Q. oocarpa* may occur as almost pure stands reaching heights of over 30 m. The general aspect of this formation is shown in Fig. 6.

In the Montane Rain Forest, *Buddleia alpina, Hesperomeles obovata, Escallonia poasana, Weinmannia pinnata, Clusia alata, Didymopanax pittieri* and *Podocarpus montanus* are characteristic trees species. The large oak, *Quercus costaricensis,* forms dense, extensive stands dominating the physiognomy of much of this formation. Above 3,000 m *Pernettya coriacea, Vaccinium consanguineum, Hypericum strictum* and *H. silenoides* are some of the more common shrubs which, with the conspicuous dwarf bamboo, *Chusquea subtessellata,* represent a mixture of montane and páramo species (Fig. 7).

In the montane forests trunks and branches of the larger trees are usually hidden under a cover of epiphytes. Pteridophytes, bromeliads, orchids and aroids comprise a major part of these "aerial swamp" communities. The ground is covered by numerous decumbent herbs, mosses and lichens among which are species of *Alchemilla, Gomozia, Lycopodium* and *Sphagnum.* In local swampy depressions the tree fern, *Lomaria loxensis,* and the large terrestrial bromeliad, *Puya dasylirioides,* emerge from a dense mat of sphagnum moss to present an almost eerie spectacle (Fig. 8). Open and disturbed areas are occupied by *Wigandia caracasana, Cirsium subcoriaceum, Rumex costaricensis* and the spectacular, large-leaved *Gunnera insignis* and *G. talamancana.*

DISTRIBUTION AND HABITAT

Bolitoglossa subpalmata occupies an extensive range in the temperate elevations of lower Central America. It has been reported from the Cordillera Central, the upper margins of the Meseta Central and the Cordillera de Talamanca in Costa Rica and from the region of Camp Boquete in Panamá. In the lower limits of its altitudinal range, approximately 1,500 m, this salamander is encountered sporadically and is common only above 2,135 m. The species is characteristic of the tropical lower montane and montane regions in a geographic range bisected into northern and southern parts by the Meseta Central of Costa Rica.

On the Cerro de la Muerte *B. subpalmata* inhabits a broad altitudinal belt above 2,300 m on the northwestern slopes, in densities conspicuously increasing with elevation. On the southern slope it is all but absent below 2,600 m.

By comparing information from precipitation and temperatures, an obvious correlation of population densities with climatic conditions is seen. It has been generally accepted that moisture, as expressed in the amount and distribution of rainfall exerts the greatest influence on the distribution of organisms in tropical enviroments (LA RUE, 49; RICHARDS, 62) and that temperature is of secondary importance. This is only true of regions with fairly uniform surface features. Many areas of low elevations, (*i.e.*, below 1,500 m in Costa Rica) meet the moisture and refuge requirements of *B. subpalmata*. Even greater rainfall is characteristic of certain coastal regions of the country, yet lowland tropical wet forest areas are not occupied by this species. Apparently temperature is the dominant physical influence in restricting the distribution of these salamanders. No limiting biological factor can yet be suggested. The species has not been observed to occupy habitats on tbe Cerro de la Muerte at biotemperatures higher than 15.2° C. I do not imply that microclimate of habitats is measurable by records from weather stations, but certainly microclimates are influenced in a general way by gross climatic regimens (GEIGER, 27).

HABITAT SELECTION

Within its altitudinal range, *B. subpalmata* occupies diverse habitats. In the Tropical Montane Rain Forest, where temperatures and evapotranspiration limits pose no problem, the shallow cover provided by litter and rocks is a common retreat. The Cerro is subject to surface drying during winter, but salamander populations need migrate only a few centimeters below the ground surface in crevices and root-fractured crannies to avoid desiccation.

In middle elevations, roughly between 2,400 m and 2,700 m, the selected habitats are quite different. The dense carpet of sphagnum and club moss that retains a high moisture level and a stable, relatively low, temperature is a habitat most frequently utilized. Occasionally salamanders may be encountered under rocks and plant debris, but only when these are deeply imbedded in the soil or possess a well-developed lichen-moss margin. Where local stream bank topography or persistent rains modify local moisture conditions, habitats that would otherwise be unfavorable can be occupied temporarily.

Below 2,400 m *B. subpalmata* was never taken in the habitats described. Crevices in moist, clayey soil on well-drained slopes were the most successful collecting sites. Such places offer an excellent balance of excess water run-off and high retention of soil moisture. Here, 8 to 15 cm below the ground surface, favorable moisture and temperature conditions are present throughout the year.

HABITAT UTILIZATION

The greatest concentrations of individuals occur in such habitats as described, although vagabonds may extend the complexity of habitat utilization. It is well known that *B. subpalmata* is an occasional dweller in epiphytic bromeliads of the "aerial swamp" (DUNN, 24; PICADO, 57). During its nocturnal wanderings, the species has been observed emerging from bark crevices in trees and logs and climbing on the branches of shrubs and moss-covered trees to heights of two meters above ground level. Most frequently, however, it is seen moving slowly over the ground or rocks in the near vicinity of cover.

In daylight hours the animals retreat to dark depressions under rocks and debris; lie concealed under dense decumbent mossy mats or deep within decaying logs; or worm their way through deep fractures and crevices in the exposed rock mantle. In view of its ubiquitous use of the habitat area, *B. subpalmata* must be at once considered as subterranean, surface-dwelling and arboreal.

LIFE HISTORY

REPRODUCTIVE CYCLE OF MALES

The testes of *B. subpalmata* exhibit a lobed arrangement similar to that of the genus *Desmognathus* (HUMPHREY, 43). Both he and ORGAN (56) have reported as many as four lobes in some species of that genus, but in 413 males of *B. subpalmata* I examined, no more than three were found.

Aside from gross dissection of the above sample, information was obtained from microscope slides of testes from 165 males. The pattern of maturation of sperm cells and lobe formation has been treated in detail by BURGER (12), HUMPHREY (43) and KINGSBURY (47), for the north temperate plethodontid genera *Desmognathus* and *Plethodon*. *B. subpalmata* has the same basic pattern, but there are significant differences.

Active meiotic division and the presence of sperm in testicular lobes and vas deferens can be seen in microscope slides of gonadal tissue from samples taken at all months of the year. As in *Desmognathus* and *Plethodon*, the primary germ cell cord gives rise to the first testicular lobe which includes numerous small lobules. In the earliest stages of formation the lobules appear to contain spermatogonia II. Since no well-formed lobules (*i.e.*, with a complete margin of septal tissue) contain cells in earlier mitotic phases, the formation of the septa and late spermatogonia seems to take place at about the same time. By the time the septal boundary is completed and the lobule well defined, some germ cells are approach-ing the spermatocyte I phase. Each of these lobules undergoes maturation as a unit, with newer lobules being continually added anteriorly.

As a result of this pattern of formation, mature sperm first appear in the most posterior part of the lobe and gradually develop more anteriorly as adjacent lobules mature in sequence. The spermatogenic "wave" is actually a series of phases in the meiotic process, each of which is confined to a single lobule.

A fairly constant pattern of transition of germ cells can be observed within the testes of *B. subpalmata* (see Figs. 9 and 10). The transitional stages from spermatogonia II to spermatocytes I usually occupy the greatest part of the testes, except for terminal primary lobes, in which maturation in the anterior portion has been completed. The region occupied by lobules containing spermatocytes II is relatively narrow, indicating a rapid transition from spermatocytes I to spermatids. Lobules composed of spermatids and spermatozoa usually occupy a region about equal to that of spermatocytes I. This implies that spermatocytes I and spermatids require a longer period of maturation and transformation than the mitotic division of spermatocytes II.

As the testis becomes fully developed, more lobules produce spermatozoa which are liberated to the central duct. In some animals all lobules may be in an advanced stage. After liberation of sperm the lobules degenerate and atrophy. The lobe then continually moves forward as the primary germ cell cord is activated. In a sense the lobe matures itself into non-existence. The posterior degenerated region becomes tbe caudal germ cell cord of temporarily "sterile" tissue. This region, which is the basis of the lobed nature of the organ, will eventually become reactivated and give rise to spermatogonia and the interstitial septa of the secondary and tertiary lobes in the same manner of development as the primary. Usually, the posterior lobe arises before the complete maturation of the lobules in the anterior one. Advanced stages of reduction division are not always present in the second and third lobes of testes, depending upon the size of the lobes; nor is it equally present in the right and left testes of a single animal.

REPRODUCTIVE CYCLE OF FEMALES

Ova are first distinguishable when about 0.1 mm in diameter. As maturation continues they gradually increase to an observed maximum diameter of 3.5 mm before oviposition. With the increased accumulation of yolk, the egg becomes cream-white in color. Definitely, not all of the ova mature. In earlier stages the number visible ranges from 19 to 71 in a single ovary, but during the later stages a size differential becomes conspicuous as some neither accumulate yolk nor significantly enlarge. The average number of apparently "ripe" ova ($>$ 2.5 mm diameter) found in a single ovary was 15.2 ($\pm$ 1.3 standard error) in a sample of 40 females. By comparison, the average number of eggs (22.6) observed in 31 clutches indicates that both ovaries mature and ovulate during the breeding period. Because of the great number of minute ova present in early development, it has not been feasible to determine what proportion actually mature and are laid; however, it is a relatively small part of the total that acquires any quantity of yolk and pass into the oviduct during oviposition. Some indication that immature ova are retained and may subsequently mature is offered by five brooding females that contained numerous small to medium (0.6 to 2.0 mm diameter) whitish ova in the ovaries.

The oviducts of mature individuals are enlarged, thickened, highly convoluted tubes which occupy much of the abdominal cavity. In immature specimens they are thin and straight dorsolateral tubules.

Females of *B. subpalmata* do not reproduce every year. Individuals with enlarged ova were found at all times of the year, but most of the marked adults did not become gravid during the period of study. Two marked females remained gravid over a period of eight months without any intervening oviposition. Unfortunately, no information is available on marked gravid animals that subsequently were noted as "spent". The female element of the population is capable of breeding throughout the year. Although in certain months a greater number of gravid females was observed, the actual proportion in total sample size did not notably differ.

OVIPOSITION

The single occasion of egg laying observed in *B. subpalmata* occurred in an adult female which had been subjected to a subcutaneous gular implant of a single anterior hypophyseal lobe of fresh *Rana pipiens* pituitary on May 9, 1962. After implantation, the salamander was kept on moist filter paper in a covered, 10 cm culture dish placed in a darkened room at 20 to 22° C.

Approximately 72 hours later, oviposition began with the extrusion of a single egg; within the next few minutes two more were delivered. The female spasmodically arched her tail just behind the cloaca and lifted the pelvis by extension of the hind limbs before oviposition. Erratic spasms forced the eggs down the oviduct to the cloaca and relaxation of the sphincter permitted extrusion of the ova either singly or in series. Upon emergence of the last egg, it was "pinched off" by contraction of the cloacal lips.

During a period of four and one-half hours, the female laid eight eggs and at intervals moved freely about the moist container. She then collected the eggs into a small clutch by use of her tail. Ten hours after the last was extruded she died, probably from hormonal shock. At this time four undelivered eggs were visible in the abdominal cavity.

NESTING SITES

Eggs of *B. subpalmata* are deposited under well-imbedded rocks or decaying logs. In these natural depressions no excavation or modification of the site is apparent. The size of the nesting site needs only to be large enough to accommodate the parent and egg clutch. The site is usually located where there has been no physical disturbance for several years, since the surface is covered with a mat of well-developed lichen and moss colonies. Occasionally, nesting sites are found in mounds or slopes of granitic talus. These too, typically, have a dense cover of low vegetation and always possess an interstitial matrix of clayey loam or gravel. On a single occasion an egg clutch was observed in a small moss-covered depression in a nearly vertical cut 3 m above a road bed.

Nesting sites are most often located about 3 to 8 cm below the surface. In only one instance was more than a single clutch found in a nesting site. Within a decomposed talus slope three clutches with the attending adults were found under the same rock fragment, each clutch nearly in contact with the others. The stages of development were well advanced and essentially equal, indicating that they had all been deposited at nearly the same time.

The egg mass is usually laid along the sides or margins of the site. The combination of clutch position and soil texture provides adequate drainage of surplus water and yet offers a high degree of moisture retention. Under protective cover and at observed depths of from 3 to 22 cm, relatively stable temperatures exist. Ambient soil-air interface temperatures recorded at 15 nest sites range from 9.8 to 16.0°C. (mean 12.8°).

EGGS AND EGG CLUTCHES

Eggs and egg masses are similar in appearance to those described by STEBBINS (70) for *Ensatina eschscholtzi.*

Two gelatinous membranes surround the opaque yolk, which almost completely occupies the cavity formed by the inner membrane. The inner membrane is not visible in newly deposited eggs; however, after immersion in water for approximately one-half hour the margins can be distinguished. The scale of measurements shown in Fig. 11 are based on pre-immersion size. An inner membrane (b) surrounds the ovum (d) and is only slightly separated from it (c). Of the two gelatinous layers the inner conforms to the spherical shape of the yolk mass and is essentially uniform in thickness. Because of variable thickness in the outer membrane (a) the egg assumes a subspherical shape. The greatest over-all dimensions are usually at right angles to the polar axis.

Eight eggs deposited by the experimental female ranged from 4.7 to 5.3 mm (average 5.0 ± 0.12 mm) in greatest diameter. These dimensions are essentially the same as for recently deposited eggs observed in the field.

The egg mass is an irregular, grape-like cluster lacking any stalk, and lies loosely within the nest site or adhering to exposed roots. The eggs are usually firmly attached to each other as a result of cohesion of the gelatinous membranes during deposition or shortly afterwards. This substance gradually hardens to some degree and forms a tough, yellowish, parchment-like surface that is less than transparent.

In 31 clutches found, the eggs numbered 13 to 38 (average 22.5 ± 1.2). Egg masses at various stages of development were found each month during the study period except for April and May. Each clutch was attended by an adult. Numerous attempts were made to observe a complete sequence of development in the field without success. Although disturbance of the nest and eggs was kept to a minimum and observations made as infrequently as but once every two weeks, the brooding adult invariably abandoned the clutch. Following this, the eggs ceased development and decomposed.

When found, four of the egg clutches were attended by males. Thirteen clutches were maintained in the laboratory with the accompanying adult, one of which was a male. No distinctive features were discerned in the brooding behavior of the sexes.

The attending parent usually was coiled tightly about the egg clutch with the forelimbs and throat region resting on the upper surface of the mass. This embrace was usually sustained for three or four days without notable change. During the period of brooding the adult seldom left the eggs and was almost always in contact with them. At intervals of several days the adults were observed to rotate the clutch with the forelimbs and tail, but changing its location little or not at all.

Evidence from both laboratory and field studies indicates that persistent, but not constant, attendance of the eggs by an adult is a requisite for their continued development under natural conditions. In captivity adults were observed to leave the clutch on occasion and to wander about the container, presumably foraging for food. (The digestive tracts of three freshly captured brooding females contained parts of insects.) Lack of constant attendance is most convincingly established by the presence of a male in the absence of a female.

EMBRYOGENESIS

No cleavage is visible in newly deposited eggs. The earliest stage recognizable without sacrifice of the egg is that of the neural groove. Optic vesicles and lens appear soon after convergence of the neural folds and undergo rapid enlargement, becoming the most conspicuous feature of the post-neural embryo. Anterior limb buds, mouth parts and gill filaments, arising as outgrowths from the gular fold region, appear at approximately the same time; the posterior limb buds being apparent somewhat later. By the time these hind buds are present the embryo is very elongate, extending over about three-fourths of the yolk circumference. The gills grow more rapidly at this stage, elongating and trifurcating from a single basal stalk. Pigmentation becomes more obvious as melanophores develop along the mid-cranial region and to a lesser degree along the lateral body margins to the tail tip. Melanophores are at first absent from the vertebral region and limb buds. Occipital and internasal fontanelles are still conspicuous at this stage. Drawings of some major features of embryogenesis are presented in Figs. 12 through 19. (In each of these figures the horizontal line represents a scale of one mm.)

As the limb buds elongate articulations and digits become distinguishable. The gills become somewhat reduced in overall size although the distal branches are more diverticulate. Distinct segmentation of the abdominal region occurs as the costal folds develop. These appear as separate ridges overlying the yolk mass which occupies the ventral region between the limb girdles (Fig. 18). Pigmentation rapidly expands over the head and body region, costal ridges and hind limbs; it is almost absent from the forelimbs. Nasolabial grooves are also distinct.

At least two weeks later, the head takes on a definitive shape, the gular fold becomes conspicuous and the feet well formed. Although variable, a reduction in gill filaments may occur as the basal portions are gradually resorbed with a concomitant fusion of the costal ridges. At this time a short yolk stalk extends from the post-pectoral region. Just before hatching the yolk mass is externally visible as a slight ventral extrusion. Pigmentation at this time is well developed with recognizable melanophores, iridophores and erythrophores. The young salamander occupies the entire central cavity of the egg and lies tightly reflexed in a head-to-tail position (Fig. 19).

I have not been able to follow the entire sequence of development in relation to time. On the basis of comparative observations of the periods involved between various and overlapping stages in different clutches, it seems probable that four to five months are required for intraoval development. This estimate is similar to that given for *Ensatina eschscholtzi* by STEBBINS (70). Moreover, the meroblastic cleavage pattern of the large, nearly isolecithal yolk and the prolonged intraoval period in absence of a free larval stage are consistent with his observations of that species.

HATCHING

One clutch of 22 eggs and another of 13 were successfully brought through hatching. These had been maintained with the attending adults at 10 to 15° C in covered plastic containers partially filled with moist soil and moss.

Emergence from the egg was usually preceded by spasmodic movements of the young as it changed position within the capsule. Moments afterwards a sudden, convulsive, extension of the entire body ruptured the confining membranes, which then collapsed from loss of internal pressure. Usually the head or tail regions were exposed at first and the offspring remained still for several minutes before throwing itself free of the capsule by a second convulsive extension. Sometimes the initial opening was large enough to permit complete emergence. Of 35 cases observed, the period from first rupturing of the capsule to emergence varied from five seconds to 17 minutes. In one of the clutches seven days elapsed between the hatching of the first and last eggs. Measurements of standard legth of the hatchlings were obtained within six hours after emergence and ranged from 9.2 to 11.0 mm (average 9.97 ± 0.10 mm).

At emergence the abdomen is still open along a narrow ventral suture exposing the small remaining yolk mass. The fragile allantoic gills may or may not be torn off as the animal forces its way through a narrow opening of the capsule. Their subsequent loss results from abrasion against the soil or moss in the microhabitat. For a few hours after loss of the gills, slight scars remain at the lateral margins of the gular fold. The first definite response of the new born is to seek cover in a moist, darkened retreat. No tendency for aggregation has been observed. The attending adults, both females, evidenced no interest in the hatching process nor in the young.

GROWTH

Field records on growth were obtained from 290 recaptures of 136 marked specimens. Of these, a total of 87 animals whose capture periods represent six months or more are presently considered. Individual growth increments during periods of from six months to one year ranged from zero to five mm. During the final field study of October, 1963, fourteen of sixteen salamanders collected at Populations II and III were identifiable from toe clips made up to 26 months earlier. Measurements at time of capture and last recapture for these animals are given in Fig. 20. The range of growth demonstrated by the seven males in this series was from 2.5 mm (attained in 15 months) to 6.0 mm (in 17 months) and by seven females, from 3.2 mm (by one individual in 15 months and by another over 26 months) to 9.0 mm (in 25 months).

Ideally, growth chracteristics should be studied on the basis of repeated measurements of individuals of known ages at regular intervals over a prolonged period. In most populations, however, the opportunity to combine all of these desiderata is rarely available. Among salamanders, the small size of hatchlings makes them almost impossible subjects for marking and their relatively infrequent capture provides limited information. Because of the continuous reproductive pattern of *B. subpalmata,* unique problems are presented that have not been encountered in studies of cyclic extratropical plethodontids. No young of the year nor other age classes can be directly assigned. Thus, actual growth increments cannot be applied to any age category without first establishing by indirect methods a basis for estimating age. The only available procedure is to convert the observed increments to annual rates for a comparison throughout the known size range for the species. My analyses and projection of the information are therefore based upon mean growth trends at the unavoidable cost of attention to individual variation.

The relationship of computed growth rates to one mm size classes is plotted in Fig. 21. Among records obtained for animals ranging in size from 35 to 54 mm were 12 that demonstrated no measurable growth over a period of from six to ten months (an additional 21 specimens did not increase in size during intervals of from one to five months). These examples occurred throughout the year and contribute to an expression of erratic patterns in which periods of negligible size increase, if any, alternate with those of more rapid growth Although zero values in a way vouch for the observed slowness of growth in *B. subpalmata,* they are of little use in the determination of annual rates, since all animals of more than ten months of record demonstrated a size increase. Thus, estimates of annual growth rates must exclude those for which no increase was noted. Information is available for 75 of the 87 records shown in Fig. 21. For the 21 males in this group the average annual growth rate is 2.87 ± 0.34 mm (range 1.3 to 6.0), for 47 females it is 2.91 ± 0.23 mm (0.6 to 7.0), and for the seven juveniles 3.00 ± 0.58 mm (1.3 to 6.0). Tests for variance among these rates support a null hypothesis that no differences exist among the three groups at the 99% confidence level.

Fig. 22 gives the average annual growth rate for each one mm size class, omitting specimens for which there was no measurable growth. Although a margin of error is inescapable, these averages would have to be treated as excessive at those intervals for which zero increments were noted (cf. Fig. 21). The broad scattering and absence of any trend among the plotted values indicates that no correlation exists between size and average annual growth rate. Within the extremes of 22 and 62 mm standard length for 75 animals the average annual increment is 2.91 ± 0.18 mm with extremes from 0.6 to 6.0 mm.

Evidence from limited field observations not meeting the six month criterion used previously suggests a more rapid growth rate, approximating five mm per year, during the period from hatching (average 10 mm) to the attainment of 20 mm average size. It may be that large adults, those over 60 mm, have a reduced annual increment as they approach maximum size.

In spite of existing limitations, it is within the purpose of this work to present an estimate of the growth curve of *B. subpalmata* to establish some basis for reasonable speculation on size-age class relationships. Applying the function $Y_t = Y_0 + K_t$, where Y_0 = initial standard length, K = the additive growth rate, t = elapsed time (one year), and Y_t = standard length at the end of t, such a curve is simply derived. What appears to be a liberal estimate for the value for K (based upon the calculated average growth rates) is 2.9 mm per year.

The growth curve constructed for *B. subpalmata* in Fig. 23 exhibits a straight-line increase in an arithmetic plot of the observed range between 22 and 62 mm. From the hatchling size at ten mm to the attainment of 20 mm the rate of increase, or value of K, is estimated at five mm per year and is therefore shown as curvilinear in this part of the range. Beyond 62 mm no information is available which permits quantifying any modification of the projected line.

SEXUAL CHARACTERS

As is typical of several species of the Plethodontidae and some members of the Salamandridae, *B. subpalmata* possesses lobed testes. The character of lobing is best known in the plethodontid genus *Desmognathus* (BURGER, 12; HUMPHREY, 43). However, the lobes in *B. subpalmata* are limited to but three instead of four as in that extratropical genus. A degree of variation is demonstrated both in size and number of lobes for each testis in a single animal. In 1.2% of 413 males, one of the testes exhibits one lobe more than the other. A difference of more than one lobe has not been observed. In such cases the extra lobe is usually small and immature, *i.e.,* not producing spermatozoa.

In mature males premaxillary teeth protrude beyond the outer lip margin, and the conspicuously truncated snout is bordered by swollen ridges on either side of the nasolabial grooves which extend well below the labial margin. An enlarged, disc-like mental gland occupies the anterior region of the lower jaw. The inner cloacal margin is lined with conspicuous papillae.

Mucous glands occurring over much of the dorsal body surface are concentrated over the cheek and scapula and are even more dense along the dorsal base of the tail. NOBLE (53) has attributed courtship stimulation as the role of these "hedonic" glands in male plethodontids. Their function in courtship has been inferred by ORGAN (54, 55) for two species of *Plethodon*, and by STEBBINS (70) for *Ensatina eschscholtzi*.

In my series of *B. subpalmata*, females attain a maximum standard length of 69.0 mm, 4.0 mm greater than that of the largest male. The snout is more rounded than in males and nasolabial grooves are inconspicuous. Membranous folds line the margin of the cloaca. Near-terminal gravid females comprise the largest size class of all specimens observed.

Swollen cloacal lips are characteristic of both sexes when in breeding condition. This manifestation, however, is indicative only of the actual breeding period of the individual and its absence cannot be used as a general criterion for reproductive immaturity. It does serve as a useful character in determining the duration of the breeding cycle in the population. Throughout the period of field study, males and females were observed in this condition.

POPULATION DYNAMICS

ACTIVITY

After preliminary investigation to determine the extent of nocturnality in *B. subpalmata*, studies on activity cycles were initiated one hour before dark and continued until after sunrise. At least two sites at different elevations were visited every two hours during the night. A total of 13 site studies were made. To investigate the possible influence of seasonal changes upon activity, these studies were conducted in October, December, March, May and July of 1961 and 1962.

B. subpalmata is completely nocturnal. Diurnal activity has been induced or stimulated to a degree by rainfall in some species of plethodontids such as *Desmognathus ochorophaeus carolinensis* (HAIRSTON, 43), but precipitation has not been observed to influence activity periods of salamanders on the Cerro before the onset of darkness. Deep within the forest, or in some densely vegetated quebradas, it is possible that lighting is so reduced even during daylight hours that some diurnal activity may be stimulated by increased atmospheric moisture. On one occasion, March 17, 1962, an exposed juvenile was collected on a talus slope near the summit between 12:30 and 1:00 PM. There had been no rainfall during this day. At the time of capture the ground surface temperature registered 12.6° C; cloud cover limited visibility to 20 meters and the relative humidity was 100%. It should be noted, however, that such conditions are typical on the Cerro, especially during late morning or early afternoon.

Activity periods may extend throughout the night, beginning just after dusk and terminating with the first discernible light of dawn. Variable emergence times were evident within the same sample areas on different nights and at different sample areas on the same night. Time of initial emergence ranged from 6:15 PM to 11:30 PM (GMT-6). At this latitude (10° N) there is only a one hour difference in the yearly extremes of photoperiod. Therefore, darkness alone cannot be the stimulus triggering activity.

Components of activity periods are highly variable. The initiation, peaks, and cessation of activity are all subject to environmental influences, principally local weather conditions, but do not seem to be modified by seasonality of climate or moon phases. The population is active during all months of the year. Because of their negative reaction to light from the headlamp, it has not been possible to determine whether emerged animals are "resting" or "foraging" during the time of observation. If exposed for more than 15 to 20 seconds, the salamanders started to move from the illuminated area. It is reasonable to assume, however, that when *B. subpalmata* emerges from its diurnal retreat it does so for some type of activity such as feeding or reproduction.

Soil-air interface temperatures taken during activity studies ranged from 0.4 to 12.8° C, whereas the range of temperatures at which any activity was observed was between 6.0 and 12.0° C. On several occasions interface temperatures favorable for emergence in the earlier hours of the night became depressed to 6.0° C or less. Activity correspondingly decreased, and below 6.0° C it ceased entirely. Behavioral responses at < 6.0° C were examined in other sites where salamanders were abundant under rocks at ground surface. Upon exposure animals demonstrated only a slow and retarded righting response.

Nocturnal relative humidity measurements ranged from 18 to 100%, but no animals were active below 51%. Low humidity probably rarely limits population activity. Recordings below 50% were obtained on only one night and were accompanied by near freezing temperatures. In general, activity seems to be correlated with high humidity. Of 36 occasions during which activity was observed, 33% occurred at relative humidities between 98 and 100%.

One night was unique in that no activity was observed at a study site. On December 27-28, 1961, near the summit (3,200 m) relative humidity dropped rapidly from 86% at sunset to below 80% by darkness. Throughout the night the humidity fell until dawn, when it measured 18%. Interface temperature at sunset was 10.0° C, but dropped to 0.4° C by 10:00 PM and frost formed on the ground surface. Such low extremes seldom occur and then in only very restricted areas on the Cerro; there is no extended effect on the total population.

Activity peaks, those periods with the greatest number of emerged individuals, occurred between the first hour of darkness (as early as 6:15 PM) and 1:00 AM. Maximum activity levels for any night were never observed when the humidity was less than 80%. The optimum saturation range was between 85 and 100%, with 12 peaks (75%) recorded within these values. Four activity peaks were observed during dense ground level fog (100% humidity) but activity notably decreased during actual rainy periods.

Curves constructed for nocturnal activity cycles exhibit both unimodal and bimodal patterns. In bimodal curves the peaks were never equal. Variations in the amount of activity occurred at all study sites. Local weather conditions on the Cerro are, as stated earlier, subject to conspicuous, sudden fluctuations. Bimodal activity patterns were almost always a reflection of measurable weather variations. The gradual increase of activity of the salamanders to a single maximum peak was modified by the onset of precipitation, at which time the total number of exposed animals became reduced. Upon cessation of rainfall there was usually a second peak which may or may not have been greater than the first, depending upon time of occurrence, intensity and duration of rain.

The characteristics of activity patterns can be examined in Figures 24 and 25, which include information obtained at the sites of Population III (2,926 m) on the night of September 18-19, 1961, and from Population II near the summit on May 12-13, 1962. Soil-air interface temperatures, sky conditions, relative humidities and percentages of total activity are given for each two hour interval from before dusk until after dawn.

In the unimodal curve (Fig. 24), activity was first observed at 7:30 PM and the single maximum took place between 9:30 and 10:00 PM, although some salamanders were active at the last pre-dawn visit at 4:00 AM. No rain occurred during the night, but ground level clouds maintained a saturated atmosphere until about 8:00 PM after which the skies remained clear.

In comparison, the influence of precipitation upon degree of activity is indicated in Fig. 25. The first animals emerged just at dark and the first peak occurred at 8:30 PM. From that time until 12:30 AM the level was reduced but again increased to a second, lesser peak at 2:30 AM. Here the initial activity peak reached its maximum at a relative humidity of 80%. The activity level was reduced as humidity decreased. After the decline of activity, a second peak occurred immediately following a period of light rain and may have been stimulated by it. A higher level might have been attained following the 2:30 AM observation, but during the 4:30 AM visit the early light of dawn obviously reduced activity.

Because the illumination and handling necessary to identify specimens would have influenced their activity, it was not feasible to determine the actual length of time most salamanders remain active during a single night. Certain individuals, however, were easily recognized by their size and distinctive color. None were active for more than two study intervals, or a period of four hours, during the night. If the time between study intervals is added to the first or last sighting, it would evidence a maximum activity period of six hours.

Two procedures were followed to assess the actual proportion of surface activity in populations. On the night of May 12-13, 1962, a sample was studied in the vicinity of Population IA and at each interval throughout the night all active animals were collected. At sunrise, after complete cessation of activity, the area was thoroughly examined and all available salamanders taken. If only this surface or available population is considered, 11.7% (7 of the total sample of 60 individuals) was active.

During activity studies at the marked population sites no animals were collected. Therefore, each interval included some animals that were observed and recorded more than once. To avoid any multiple records of active individuals I have used the period of greatest activity during any one visit to estimate the degree of activity in the population. The number of active individuals compared with the total observed salamanders in a marked population within a week of the night study gives activity levels from 19.8 to 24.6%. If observed activity levels are compared with predicted numbers of individuals in the study areas computed from capture-recapture data for months during which activity studies were made, the proportion of activity is reduced to a range of 0.002 to 0.050% of the total population.

At the maximum less than a quarter of the population is active in any one period. No correlation in the intensity of activity with seasonal climatic regimens has been demonstrated, although local weather conditions do influence emergence on any given night. Furthermore, I have obtained no evidence which correlates differences in periodicity or levels of activity with sex or sizes of individuals.

MOVEMENTS

Throughout the range of *B. subpalmata* on the Cerro de la Muerte, there is a high carrying capacity sustained by the available habitats. Diurnal retreats are practically always available to the animals within a distance that can be traversed during a nocturnal activity period. Spatial utilization of the total habitat is three dimensional. Potential retreats are not only immediately beneath surface cover, but also include subterranean levels to depths of probably a meter or more in talus deposits. During periods of activity salamanders primarily utilize the ground surface, but also have been observed climbing on rocks and logs or in shrubbery. The arboreal habits of the species have already been mentioned.

Collections of subsurface specimens offer some information as to the degree of vertical movements within the substratum. One excavation of a square meter area produced negative results, while another produced 25 individuals taken from cavities and crevices in rocky soil to a depth of 30 cm. On another occasion fourteen adults were taken from within a rotting log approximately 2 meters in length and 30 cm in diameter.

I assume that three-dimensional movements are taking place during normal activity of the species within its home range. Repeated capture of the same individual at the same site after intervals in which it was known to be absent can only be accounted for by subterranean activity.

Measurement of movements have been based upon straight line distances between refugia. Although not taking into account the three-dimensional nature of activity or wandering between retreats, these records offer a basis for evaluation of the comparative degree of mobility of individuals. Records were obtained from a total of 269 moves of 194 marked animals present at the five natural population sites. These individuals were recaptured from one to as many as eight times.

By assigning the moves of *B. subpalmata* to discrete intervals in time and distance, statistical analysis of the relationship of these two factors can be made. Measured distances of separate moves, rather than total distance covered or net distance from a given site, were plotted in one meter units against the actual

TABLE 3

Movements of B. subpalmata *expressed in monthly intervals. The null hypothesis assumes that distances moved are random with respect to time. Chi-square values are accepted at the 95% confidence level at N - 2 degrees of freedom. Asterisk (*) indicates rejection of the null hypothesis.*

Monthly Interval	μ in meters	ε Freq.	ε Poisson Numbers	Chi Square
1	2.87	122	121.57	269.64 *
2	2.13	39	38.73	99.69 *
3	3.05	14	13.98	31.82 *
4	3.90	16	15.80	103.25 *
5	2.21	20	19.99	31.29 *
6	4.97	17	17.01	61.88 *

TABLE 4

Comparative averages of distances moved by males, females and juveniles. The null hypothesis assumes no significant differences between any of the three groups. Chi-square values are accepted at the 95% confidence level at one degree of freedom.

Males	Females	Juveniles	Chi-square
5.43	3.71		0.1637
5.43		2.85	0.4119
	3.71	2.85	0.0566

TABLE 5

Comparative averages of number of separate moves of males, females and juveniles. The null hypothesis assumes no significant differences between any of the three groups. Chi-square values are accepted at the 95% confidence level as one degree of freedom.

Males	Females	Juveniles	Chi-square
1.19	1.53		0.0209
1.19		1.13	0.0007
	1.53	1.13	0.0299

period of time in months between two captures. Of the total moves observed, 228 which cover periods from one to six months, were compared separately with a Poisson distribution to obtain an estimation of the nature of randomness in movement. Table 3 includes pertinent values derived from these calculations.

The value of μ is the average distance in meters moved for all animals during that time interval. Chi-square computations are derived by use of squared deviations from the Poisson number for each distance interval. In all time intervals the distances moved are rejected as being random on the basis of Chi-square values at N-2 degrees of freedom for the samples, each greatly exceeding the 95% confidence level. If the distance of movements increased randomly with time, it would indicate that individuals do not occupy any defined area. The distances are not random, however, implying that a home range is utilized.

Field records on movements of unsexed juveniles ($<$ 30 mm standard length) included 15 animals. Of a total of 17 moves, the extremes were 0.10 and 13.2 m. In adult males the limits of 75 observed moves of 63 specimens ranged from 0.10 to 50.39 m and for 177 moves of 116 females between 0.05 and 35.13 m. To evaluate this information distances have been assigned intervals of one meter at frequencies of occurrence for juveniles, males and females (Fig. 26). This procedure disregards any time interval.

Among juveniles the average distance of all moves is 2.85 ± 0.84 m, with an average of 1.13 moves per individual. Adult males average a distance of 5.43 ± 0.97 m with 1.19 moves per specimen. The magnitude of each move by females averages somewhat less, 3.71 ± 0.42 m, than for males but the average number of moves per individual is slightly greater, 1.53.

Averages of the distance of movements (the null hypothesis being that the difference in magnitudes are not significant between juveniles, males and females) are treated in Table 4. In each of these comparisons the null hypothesis is substantiated at the 95% level for one degree of freedom.

On the assumption that no significance exists in differences of the number of moves per individual in juveniles, females and males, Chi-square evaluation again substantiates the null hypothesis at the 95% probability level with one degree of freedom (see Table 5).

The relationship of distances moved to sizes of the salamanders can now be examined. In Fig. 27 the average of observed distances of moves for each two mm size class is plotted for juveniles, males and females. Within ten mm size intervals, males of 30 to 39 mm standard length are represented by 12 records; those between 40 and 49 mm by 57; from 50 to 59 mm by five and those above 60 mm by one. Females of 30 to 39 mm included 42 observations; those from 40 to 49 mm included 60; from 50 to 59 mm, 62; and above 60 mm, 13. Intervals for which there were few records demonstrated the higher averages. The pattern of these results does not suggest any correlation between size of the animal and average magnitude of movement.

The extent of mobility in size clases of *B. subpalmata* is presented in Fig. 28. Plotted at two mm intervals of standard length, again for all three groups, are the average number of recorded moves. Here also, the values generally reflect size classes of animals most frequently captured. The inconsistent overlapping or close proximity of values does not evidence any correlation between size classes and mobility.

HOME RANGE

There is little information available on salamander home ranges. This aspect of amphibian ecology has been considered only incidentally by most workers who have used variable treatments. To define this concept I have depended heavily upon the interpretations of BURT (13), DICE (20) and FITCH (25).

Certain types of movements have been considered to be exclusive of home range areas. BURT (13), for example, has stated that "occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range". In his work on *Rana pretiosa* in Yellowstone Park, TURNER (74), treated cyclic migrations and rapid population shifts as part of the "activity range" but beyond the normal limits of what he referred to as a "fixed home range". Such seasonal wanderings are well known in all terrestrial vertebrate groups. It must be recognized that distinctions between rapid shifts or temporary excursions are characterized more in magnitude of time rather than distance (omitting, of course, long-range migrations). CUNNINGHAM (17) has pointed out that the essential difference between temporary extended sorties and the possession of two home ranges is that of time.

As here conceived, the home range of *B. subpalmata* includes that area within which the individual persistently carries out its normal role in the community. As no breeding migrations or aggregations occur in this species, the only activity which is not construed to be within a home range is movement that may be associated with dispersion of the population. In the absence of any known territoriality, and considering that there is seldom a limitation on habitat space or a distance between sites of protective cover in excess of the average distance of moves, the home range is viewed as being essentially circular.

I have adopted in part the methods for determination of home range areas defined by FITCH (25) in which two different types of measurements can be utilized: (1) the observed distances between two successive sites of capture of an individual, and (2) the longest (net) distance between any two capture points. This procedure offers the advantages of permitting determination of the average home range of members of the population from limited individual recaptures and a comparison of the size of minimum home range areas of individuals estimated from the net of total recorded distances. Certain disadvantages are inherent in any application of these measurements. They do not offer any indication of the extent to which some parts of the home range are subject to greater use than others, and the straight line distance between two points of capture represents only the minimum, or net, change in position.

The average home range area is computed as the area of a circle (πr^2) using straight line distances (radii) recorded in 290 recaptures for which measurable position changes ($>$ 0.05 m) were available. Radii extremes (0.05 to

50.39 m) are therefore equal to those obtained for separate moves; area extremes would be from 0.008 to 7,977.00 sq. m. The average home range radius is 3.74 ± 1.19 m and the average area is 43.6 ± 4.44 sq. m. As no statistically significant differences were found in comparing moves of juveniles, males and females, these averages should uniformly apply.

In the absence of any contradictory evidence, I am presuming the general character of home ranges for extratropical plethodontids to be essentially the same as that of *B. subpalmata*. Measurements from the following citations have been converted to meters. In *Ensatina* (STEBBINS, 69) significant differences were observed in the average home range radii of adult males (19.5 m) and females (10.1 m) giving average home range areas of 1,194.6 and 314.2 sq. m, respectively. Sex determination has not been feasible in studies on movements of *Batrachoseps attenuatus* or *B. pacificus*. HENDRICKSON (35) gives the average "cruising radius" of the former species as 1.5 m, which would be an average home range area of 7.1 sq. m.

Animals recaptured more than once at the same site offer no real measure of the extent of home range, although this kind of information is valuable in indicating the degree of utilization of a home site. The sedentary nature of plethodontid salamanders has been commented upon in each of the above papers, but it is somewhat difficult to equate them. In the two reports mentioned above, vagility was measured with reference to changes of cover without regard to size of the surface objects or any movements occurring beneath them. STEBBINS (69) observed 39 of 527 marked *Ensatina* that remained under the same cover from one to five months during four years of study. In his work on *Batrachoseps attenuatus*, HENDRICKSON (35) introduced relatively large cover boards which permitted considerable position changes beneath them. It is possible that his value, 59% of 133 marked animals which did not change cover in 24 months, may have been influenced by this factor and would therefore be conservative. Of 375 recaptures in *Batrachoseps pacificus*, CUNNINGHAM (17) reports that 92% moved to other cover.

Evidence of the sedentary nature of *Bolitoglossa subpalmata* is based upon 22 of 406 (5.4%) recaptures in which the animals had not changed position more than 0.05 m (without regarding the size of cover) in periods up to ten months. No significant differences could be noted as to sex or size. An adult female, taken nine times during a twelve month period actually changed location between each observation, but the sum of all moves totalled only 6.4 m. Usually the character of movement did not demonstrate this degree of activity with such short total distance; however, the greatest distance moved by an individual (for which there were two or more recaptures) was slightly less than 21 m.

HOMING BEHAVIOR

Field experiments were conducted on nine marked adults (six females and three males) to determine the nature and degree of homing instinct. The salamanders were placed at different directions and distances (two to twelve m) from the points of original capture, and these sites were checked at six weekly intervals following displacement. In only one instance was a displaced female found in its original site, from which it had been moved three m two weeks before. This female was again removed and placed seven m away in the same direction but never was observed to return. Although no other displaced *Bolitoglossa* returned, several had been placed nearer to the capture point.

These few records can no more than suggest that homing behavior is poorly developed in *B. subpalmata*. However, the lack of fidelity in egg clutch attendance, as well as the ease with which adults abandon them, offers supporting inferential evidence.

AGGREGATIONS

Below levels of 2,500 m, population densities are low and seldom are three or more salamanders found in close proximity within the same refugium. In mid-ranges and upward to the summit area, as densities increase with more favorable environmental conditions, the occurrence of aggregations becomes more frequent. Above 3,000 m the finding of six to fourteen animals under a rock not more than 15 cm in diameter is common.

No indication of sexual behavior has been observed in the composition of aggregations. The groups were composed of all males, all females or varying numbers of both sexes with equal frequency. By following the movements of marked individuals, the composition of aggregations was observed to change markedly. On only three of 290 (1.03%) occasions were the same two animals together more than once in the same refugium.

During the dry season on the Cerro, the ground surface becomes caked and salamanders are found only under deep seated debris and rocks where moisture has been retained. Aggregations are intensified during this time. For example, between September, 1961 and February, 1962, only 17 specimens had been found at the site of Population IV. In March, however, 15 new individuals were marked, all of which were in localized aggregations. By experimental methods I have found that this behavior is of some survival advantage in lowering rates of water loss in individuals by reducing the exposed body surfaces during stress conditions.

At times of local inundation a similar type of behavior is elicited. As submergence tolerances are discussed in another section of this paper, it will suffice to state that avoidance of excessive moisture will occasionally force several individuals to use the same retreat.

DENSITIES

Most estimates of amphibian population densities have been derived from capture-recapture data utilizing some form of the proportional index method. For pertinent treatment and evaluation of such procedures the reader is referred to the series of papers by TURNER (74, *et seq.*). Available information on densities of salamander populations is notable only for the limited number of studies that deal with this aspect of population ecology and the variety of techniques employed.

B. subpalmata utilizes its habitat to a wide degree. In view of this fact, the lowest (or crude) densities and ecological densities are equated. Evidence for estimation of these parameters has been obtained from a total of 290 recaptures of 936 marked salamanders at five population sites over a one year period. Observations of relative densities are of more limited value, but they can be useful in determining general distribution patterns. Relative density estimates are based upon 695 specimens taken from 60 quarterly quadrat samples in the study area.

There is an almost constant pattern of decreasing density with lower elevations. The value for each quadrat from which specimens were taken is given in Table 6, and is obtained by computing relative density as the number of individuals per sq. m. No animals were ever collected in 20 quadrat samples from elevations below 2,438 m on the northwest slope or 2,591 m on the southern slope. In these quadrats, densities are expressed as < 0.0053, which represents the proportion of one sq. m to the total quadrat size, or 1/186 sq. m, and thus allows for the possibility of *B. subpalmata* occurring in the general area at very low densities. The extremes of relative densities in all quadrats where the species has been collected range from 0.0053 to 0.3333 per sq. m. The averages of four samples from each elevation are between < 0.0282 to < 0.1841 individuals per sq. m. Variations existing in correlation of altitude with density are not significant. Although attempts were made to equate the physical conditions of quadrats at each sampling, the necessity of using different sites undoubtedly influenced results. Also, a week or more was required to complete each sequence of samples and local changes in weather conditions are possibly reflected in the data. In spite of these sources of error, the correlation is conspicuous.

Better perspective of the altitudinal distribution of *B. subpalmata* can be gained when the relative densities of animals collected from quadrats are plotted against biotemperature levels on the Cerro de la Muerte. Fig. 29 includes all quadrat samples. The greatest densities occur in the lower biotemperature range. In all cases where there were 0.14 or more animals per sq. m, biotemperatures were below 10.6° C. Of 16 samples from sites above 15° C only 3 (19%) were ever occupied by *B. subpalmata* during the year and the highest density represented was 0.1075 per sq. m; equal to the lowest density level ever recorded at the summit.

Salamander populations on the Cerro de la Muerte are subject to conspicuous changes in densities. The impact of the January-March dry season is by far the most intense and lowest surface densities occur during this time. With the onset of April rains (refer to Figs. 3 and 4) the animals move to the surface from their subterranean refugia. Fluctuations also occur in response to shorter and less intense dry periods, as the Veranillo de San Juan in July and August. The most striking example of changes in relative numbers can be seen near the summit where optimal habitat conditions and greatest densities prevail. In samples taken from a series of quarterly quadrats at 3,048 m elevation on the south slope, numbers of individuals collected ranged from 0 to 62, representing surface densities of from < 0.0053 to 0.3333 animals per sq. m. Seasonal variations

TABLE 6

Relative densities of populations of B. subpalmata *as determined from quadrats. Values give the number of individuals per sq. m. [An asterisk (*) represents samples in which no animals were present in the 186 sq. m. quadrat.]*

Slope	Elevations in Meters	March	June	Sept.	Dec.	Ave.
NW	2438	.0645	.1129	.0053	<.0053*	<.0470
NW	2591	<.0053*	.0753	.0161	.0161	<.0282
NW	2743	.1291	.0645	.0376	.0645	.0739
NW	2896	.0645	.1508	.0753	.0753	.0914
NW	3048	.0430	.2582	.2044	.1237	.1573
Summit	3200	.1075	.1559	.1882	.1452	.1492
S	3048	<.0053*	.3333	.1183	.2797	<.1841
S	2896	.0645	.1291	.0699	.0053	.0672
S	2743	.0484	.0484	.0806	.0430	.0551
S	2591	<.0053*	.1022	.1075	.0215	<.0591
Monthly Averages		<.0537	.1432	.0903	<.0779	<.0930

TABLE 7

Comparative densities of some plethodontid salamanders.

Species	Stated Crude Density	Crude Density Ind./Sq. Meter	Source
Plethodon cinereus	202 per acre	.0499	Test and Bingman (72)
Batrachoseps attenuatus	84 per 2,000 sq. ft.	.4516	Hendrickson (35)
Batrachoseps attenuatus	3,870 - 8,160 per acre	.9558-2.0155	Anderson (2)
Aneides lugubris	1,640 - 2,020 per acre	.4051-.4989	Anderson (2)
Ensatina eschscholtzi	600 - 700 per acre	.1482-.1729	Stebbins (70)
Bolitoglossa subpalmata	306 - 3,683 per acre	.0756-.9097	

were observed in all areas where the species was found, although usually of lesser magnitudes. Similar responses to annual distribution of rainfall have been reported for the plethodontid genera *Batrachoseps*, *Aneides* and *Ensatina* (ANDERSON, 2; HENDRICKSON, 35; ROSENTHAL, 63; and STEBBINS, 69).

Computed densities have been determined by application of the BAILEY (4) modification of the proportional index method to capture-recapture records. Populations I and IA have not been included, as the information did not extend over a full year and also, these sites were at essentially the same elevation as Population III. Computations of crude, or lowest, densities available for other salamander populations have been based upon the number of individuals in relation to the actual size of the study area and presume that movements by animals into and out of the area are equated. Such a predication, however, is not entirely accurate. Unless natural barriers limit the study area, the established borders are artificial and peripheral animals will be present in varying frequencies depending upon the extent to which their home range areas overlap the boundaries. Individuals that have a major portion of their home range intersected by this margin will be encountered more frequently than those with but a small part within the defined area. In cases where peripheral animals may be present it should be recognized that the study site is really inclusive of a larger area than the measured limits, and without some adjustment the computed density values will be unrealistically high. To compensate for variations in the extent to which home range overlap occurs, a margin about the defined study zone equal to the home range radius should be added and the total area considered in relation to densities. This procedure has been used by BURT (13) in determining densities of small mammals.

Adjusted density values for *B. subpalmata* were obtained by adding the average home range radius of 3.74 m to the margins of study areas. The following area sizes in sq. m were obtained (corrected values in parentheses): Population II, 645.6 (1,225.5); Population III, 1,103.2 (1,948.6); Population IV, 878.5 (1,706.0). Variation in the proportionate increase results from differences in shape of the study sites. Fig. 30 shows the number of animals per sq. m in each population at monthly marking intervals computed on the basis of these corrected values. The BAILEY (4) formula, $N = a\ (n+1)\ /\ (r+1)$, in which a = marked individuals at risk, n = size of second sample and r = marked individuals in second sample permits computations based on zero recaptures, indicated by the open circles. These statistical artifacts (*e.g.*, $0+1$) are not considered in the following summary.

Population densities determined from capture-recapture records generally demonstrate the same positive correlation with altitude exhibited by the relative density study. Density is greatest in Population II (3,200 m elevation), having an average ecological density of 0.4795 ± 0.0556 individuals per sq. m. Population III, at 2,926 m, averaged 0.3269 ± 0.0502; and Population IV, at 2,560 m, 0.0389 ± 0.0068.

Seasonal changes in computed densities are also obvious. Annual extremes in numbers of animals per sq. m were from 0.2363 to 0.7437 near the summit. In

Population III and IV densities ranged from 0.1170 to 0.6672 and 0.0205 to 0.0516, respectively. The absence of correlation in time of occurrence or elevation is a product of local climatic influence.

In view of the nature of the defined study areas, available data on densities of extratropical plethodontids appear to be consistent over-estimates. For purposes of comparison, crude densities of *B. subpalmata* can be computed on the basis of the actual study area, rather than an adjusted value obtained by addition of the home range radius. Uncorrected densities of from 0.0757 to 0.9100 salamanders per sq. m represent the extremes of observed annual averages obtained during my studies. Table 7 summarizes the comparative data available for four other species and equates the numbers of individuals in sq. m units. ANDERSON (2) studied populations of *Aneides lugubris* and *Batrachoseps attenuatus* on the islands of San Francisco Bay, California. The average density of four estimates he obtained for *Aneides* was 1,892 per acre. His remarkable estimate of 66,530 *Batrachoseps* per acre was admittedly excessive, which he attributed to a local population shift; however, he considered an estimate of 8,160 salamanders per acre to be reliable.

If the observed activity levels of *B. subpalmata* are in any way indicative of low energy demands by these montane ectotherms, then the factors limiting the number of individuals would appear to be density-independent; most probably, spatial requirements and available microhabitats present within the distribution range.

AGE CLASSES

Age class characters of amphibian populations have usually been based upon data from large samples collected within a short period and the size classes compared, as in BANNIKOV'S studies on *Ranadon sibiricus* (5) and *Bombina bombina* (6). Several studies on plethodontid salamanders (ANDERSON, 2; GORDON, 28, 29; POPE, 59; POPE and POPE, 60, 61) have included an analysis of the composition of populations, usually in reference to the proportion of young, subadults and adults. Invariably, young animals are separable on the basis of size. As the age classes increased the number of mature adults exceeded the younger groups and became concentrated to the right of the histogram. These merging patterns in adults have complicated the interpretation of size-age class relationships of older individuals. Measurements of *B. subpalmata* population samples provide no direct evidence from which age estimates can be made. As shown from the data in Fig. 31, whenever extensive and year round information is available a pattern in size frequencies is demonstrated that lacks consistent indication of age groupings.

Testicular lobes have been used by HUMPHREY (43) and ORGAN (61) to establish age classes in *Desmognathus*. By examination of histological material of *Desmognathus fuscus*, HUMPHREY (43) determined that males with two mature testicular lobes were in their third season of sexual activity and that each subsequent lobe required two years to develop fully. Using the same time interval, ORGAN (61) defined the age limits of *Desmognathus* having one lobe as between three and four years; two lobes representing five to six years; and three lobes indicative of seven to eight years. In the five species included in his study all males matured by the fourth year after they had been deposited as eggs.

Fig. 32 includes a sample of 140 *B. subpalmata* males taken during June of 1962. The two mm interval was chosen with the purpose of avoiding any bias in favor of the proposed growth curve (Fig. 23). Single-lobed males in this sample demonstrated a modal group at the 41 mm midpoint. In double-lobed males the mode occurred at 47 mm, with a second peak at 55 mm, while the mode of the three-lobed specimens was at 55 mm. These modes may be coincidental artifacts, but they obviously conform to the estimated 2.9 mm per year growth increments derived from marked and recaptured animals and correspond almost exactly to intervals at the ninth, eleventh and thirteenth years, without accounting for any range of variation. If the biennial pattern of appearance of testicular lobes correctly applies to this continuously reproducing tropical species, then the averages represented by the growth curve are indirectly substantiated.

SEXUAL MATURITY

The capacity for reproduction is characterized in males by the presence of mature sperm in the testes and Wolffian ducts, and in females by the appearance of thickened, convoluted oviducts and large ova ($>$ 2.5 mm dia.). In both sexes maturity is attained over a fairly wide range of age and size.

From microscope slides of gonadal tissue for 154 *B. subpalmata* males between 21 and 65 mm standard length the principal phases of spermatogenesis present are recognizable. A single male of 26 mm represents the smallest individual attaining maturity. Above this size the proportion of mature males generally increases to the 42 mm size class, above which all specimens examined were producing sperm. A size difference of 16 mm exists between the onset and completion of sexual maturity in the male element of the population.

The occurrence of mature sperm in the vas deferens appears to be simultaneous with their first occurrence in the testes, although in 9.7% of the tissue preparations extratesticular sperm could not be found in mature animals. It is possible that this is due to artifacts resulting from the mounting techniques employed. If a minor fluctuation does occur in the reproductive activity of males or a period of sperm retention exists, my observations do not indicate any correlation with either size or season.

Organ (56) used thickened, convoluted oviducts as the criterion of female maturity, but Pope and Pope (60) considered these structures to be subject to recurrent resorption, at which time they appeared as straight and narrow tubules, alternating with the periods of breeding activity. In a sample of 335 *B. subpalmata* females (plotted at 2 mm intervals in Fig. 33), the size classes between 38 and 54 mm included 158 individuals with and without mature oviducts. Females above 38 mm demonstrated a generally consistent increase in the proportion of the sample that possessed this character. Of 16 females in the 54.0 to 55.9 mm size interval, 25% had never laid eggs nor did the condition of the oviducts indicate that they were in a physiological condition to do so. All 66 specimens of 56 mm or more were mature by this criterion, although in most of these the ova could be classified as minute ($<$ 0.6 mm dia.) and did not demonstrate any yolk accumulation. Five of the latter group (7.6%) were obviously spent. It is certain that mature oviducts persist once they have developed.

The condition of the oviducts does not adequately establish sexual maturity in females. Consideration must also be given to size and age of the animal when oviposition first occurs. Although mature oviducts were observed in females of 38 mm, the smallest individuals noted as gravid or brooding were in the 42-43.9 mm size class. Among 22 specimens examined in the 44.0 to 45.9 mm size class, 12 had mature oviducts; three were obviously gravid and one was brooding eggs. The minimum growth increment of an individual between the onset of maturity (*i. e.*, with mature oviducts) and the period of egg laying was 6 mm. Gravid or brooding females were represented in all size classes above 44 mm and all females of 56 mm or larger showed evidence of having previously deposited eggs or were in a condition to do so. Therefore, sexual maturity in females occurred some time within a growth interval of 12 mm.

The irregular pattern of the percentage of increase between size extremes at which maturity occurred was probably a result of the limited sample at each size interval and variability in physiological conditions of individuals. No single modal size class was present in either males or females. In Fig. 33 the 50 % maturity level of the population is shown as the median between the largest size class at which no individuals were mature, and that at and above which all specimens examined were reproductively capable. The 50% levels are represented by the intersection of the slanted line connecting the extremes of these size classes with the 50 % abscissa. For males the median is 33 mm. In females the 50 % level between initiation of maturity and the 100 % level is at the midpoint of the 46.0 to 47.9 mm interval, or 47 mm, but for the range of size at which oviposition is known to occur the midpoint is 49 mm.

By using the previous estimates for growth and age classes, acquisition of sexual maturity in *B. subpalmata* populations can be translated into time. Within this scheme the earliest maturation of males would occur at four years and gradually increase through the ninth year, by which time all males were capable of reproducing. Between these extremes, a time range of five years, the population median (50% level) for maturity in males is predicted at the sixth year.

Sexual maturity in females is considerably delayed as compared to males The earliest oviposition was after the ninth year, an age at which all males were mature, and increased until about the fourteenth year when all appeared to have laid eggs at least once or were gravid. Maiden females were present in the thirteen year age category. The time range of extremes represented here, four years, is slightly less than that of males and the 50% level of maturation is predicted at the twelfth year. The average time factor for the 6 mm differential observed between the occurrence of females with mature oviducts and the smallest size (44 mm) at which reproduction has been observed, would be approximately two years. Data offered in the earlier treatment of sexual cycles substantiate this estimate and suggest that a two year period is probably the minimum required between successive ovipositions of egg clutches.

The variation in ages at maturity in both sexes of *B. subpalmata* seems reasonable in view of the estimated 18 year potential life span. Retarded maturity in females may be a reflection of the time required for the relatively high energy demands imposed by elaboration of oviducal cells and by that required for storage of nutrients in the ova during formation. It is likely, too, that the introduction of mature females occurring at a time when all males of equivalent age are mature would enhance the probability of sexual encounters and reproductive success.

SEX RATIOS

Evaluation of the sex composition of *B. subpalmata* populations is based upon evidence from quarterly quadrats. Of 695 specimens, 681 could be sexually determined by dissection. The sex ratios at each sample period listed in Table 8 essentially represent a one to one relationship and Chi-square values substantiate the null hypothesis at the 95% confidence level for one degree of freedom.

TABLE 8

Chi-square tests of the ratio of males to females in populations of B. subpalmata *as represented by the quarterly quadrats. The null hypothesis is a one-to-one sex ratio. The data were accepted at the 95 % confidence level at one degree of freedom.*

Month	Nº Males	Nº Females	Total	Males / Total	Chi Square
March	39	58	97	.4020	1.8788
June	140	124	264	.5303	0.4853
September	87	92	179	.4860	0.0698
December	70	71	141	.4964	0.0355
TOTAL	336	345	681	.4933	0.0595

Several species of plethodontid salamanders have been reported by previous investigators to show statistically significant differences from a balanced sex ratio. These differences have been observed both in favor of the male, as in *Aneides aeneus* (GORDON, 28); and of the female in *Plethodon vehiculum, P. dunni* (DUMAS, 21) and *P. yonablosee* (POPE, 59); or changing seasonally in *Plethodon cinereus* (TEST and BINGHAM, 72). In his studies of the genus *Desmognathus*, ORGAN (56) found three of the included five species to demonstrate significant differences, each in favor of the male.

Numerous factors have been considered as operative to a degree resulting in disparities in the sexual composition of plethodontid populations. Brooding females of some species are more likely susceptible to predation *(Desmognathus)*; gravid females may be more secretive, hence a sampling error is introduced *(Aneides)*; in *Plethodon cinereus* sexual differences in seasonal activity are apparently significant; the aquatic habitat occupied by the female in some species of *Desmognathus* during brooding is a more severe environment than the terrestrial one of the non-brooding female; lack of feeding on the part of an attending female, resulting in greater susceptibility to the rigors of overwintering, may be a sexually selective factor.

None of these causes act to any significant degree in populations of *B. subpalmata.* Females with egg clutches demonstrate an escape response not markedly different from other individuals. Microhabitats utilized for nesting offer optimal habitat conditions and are commonly frequented by non-reproducing members of the population. Studies on activity cycles and movements have offered no evidence to indicate that diel or seasonal patterns are in any way different between the sexes. Although fluctuations in population densities are considerable, the proportion of males to females does not significantly change. The apparent absence of a strong brooding instinct on the part of attending females and the probable continuance of feeding during this time would eliminate these factors as being of any importance in differential survival. Lastly, the most extreme seasonal changes demonstrated during the dry period on the Cerro de la Muerte cannot be equated with the impact of protracted extratropical winters. Briefly stated, in *Bolitoglossa subpalmata* the sexes do not demonstrate differences in activity, habitat or reproductive behavior as have been reported for several plethodontids of the temperate zones, hence factors contributing to differences in sex ratios are not operative to a measurable degree.

It can be seen from the sex ratio composition of quadrats in Fig. 31 that the smallest and largest size classes are disproportionately represented. In most specimens below 20 mm it has been impossible to determine their sex, even by dissection, due to an absence of any enlargement of the germinal cord or definition of ovarian structures. Above 60 mm standard length males are conspicuous by their near absence. Specimens of 69 mm standard length have been collected in random sampling but the largest male taken from quadrats is in the 65 mm class. No evidence is available to account adequately for the apparent rarity of large males. The relatively early attainment of maturity in males and their sustained reproductive capacity in comparison to biennial cycles in females may possibly contribute to accelerated senility and death. WILLS (81) has reported a relatively higher metabolic rate in mature males of *Taricha torosa* and TURNER (74) has suggested this phenomenon to be present in *Rana pretiosa.* If any significant differential in sex ratios does exist at various stages of the life cycle, it is balanced within the total population.

REPRODUCTIVE POTENTIAL

Adult females became recognizably gravid between two observations that varied in time from two to seven months. The longest observed period during which an individual was continuously gravid was eight months. These two periods together comprise a minimum of ten months from the time of egg enlargement until deposition. A maximum period of two years is suggested by the differential between maturation of the oviducts and the youngest animals to be found brooding (Fig. 33). Probably this latter period is more accurate, for this was also the minimum time estimated to be required for the enlargement of eggs. This means that a typical adult female is capable of depositing eggs every other year after reaching maturity at the age of nine. Given the estimated maximum survival age of eighteen years, the lifetime potential would be five clutches each averaging 22.5 eggs, or 112 offspring.

An estimate of reproductive potential at the population level may be constructed from field data. Of 345 females collected in the quadrats 32 were gravid and ten were brooding. If only these ten (2.9 %) of the total females are considered as the reproductive complement of the population the estimate would be artificially low. Since no excavation was done during this sampling some of the most likely nesting sites remained intact. Addition of the 32 gravid females present (9.3 %) would probably make the estimate too high as ripe eggs may be carried at least eight months. A more reasonable basis for determining reproductive potential is obtained by combining the spent females taken in the sample (eight, or 2.3 %) with the brooding females and gives a total of 5.2 %. This procedure admittedly incorporates a great margin of error, but it cannot be avoided.

On the assumption that these 18 brooding and spent females are producing a total of 405 offspring (number of females × average size of egg clutch) then from a total of 695 males and females in the sample, 58.3 % (405/695) of the population is being added yearly. This value represents the estimated annual partial potential reproductive capacity of the population.

SURVIVORSHIP AND MORTALITY

The most simplified method for estimating mortality rates is to determine the proportion of marked animals present one year after capture. Of 34 individuals at Population II only three were found after this interval. If all of the original sample were equally at risk, the mortality rate would be 0.91 per year ($P = 0.09$). Although full-year records from other populations were more limited in numbers, approximately the same rates were obtained.

To proceed with any further examination of survival characters of *B. subpalmata* several premises must first be accepted: (1) the estimated age-class relationships are valid; (2) reproductive and death rates are equal; (3) no differences in mortality are exhibited by the sexes; and (4) no unbalanced migration patterns result in reduction or dilution of the population.

ORGAN (56) has attempted the determination of survivorship rates in five species of *Desmognathus* utilizing the character of multi-lobed testes and interpolating the age classes from HUMPHREY'S (43) estimates. On the basis of seasonal reproductive patterns in *D. fuscus* the latter worker was able to assign an absolute time interval of two years between the successive formation of testicular lobes after attainment of maturity.

The confamilial relationships of *Desmognathus* and *Bolitoglossa* make the application of Organ's procedures to the present study an obvious consideration. However, because of the acyclic reproductive pattern and apparent relatively slow growth rates in *B. subpalmata,* the results of any comparisons of survivorship with *Desmognathus* on the basis of testicular lobing must be cautiously regarded. A composite of all quadrat records has shown a wide range of overlap in the sizes at which a given number of testicular lobes may occur. To restrict the extremes of size differences at which males may form new lobes during the year, the June sample presented in Fig. 32 was taken as most applicable. Following the assumption that all two-lobed males have passed through the one-lobe stage, and all three-lobed males through the two-lobed stage, the relative sizes of these groups may offer evidence for interpretation of specific age class survivorship rates. To equate the risk of capture of all three groups only adult animals are included. The 50 % maturation level established previously includes as adults all males in the 32 mm (33 midpoint) interval and up.

Of 82 adults in the one-lobe class, 35 survive to acquire two lobes, and give a biennial survival rate of 0.427 between the ninth and eleventh years (as estimated from the modes), or an annual rate (equal to the square root of this value) of 0.65. If the six three-lobed specimens represent a true proportion of survivors of the two-lobed group, then the biennial survivorship rate of 0.086 is an annual rate of 0.29 for the eleventh through thirteenth years. It must be emphasized, however, that these estimates offer only a general indication of survivorship levels; the total age ranges of the three groups cannot be evaluated further.

Life tables and survivorship curves are difficult to establish for animals of considerable longevity unless the number of deaths is a fairly characteristic change with each age group. Because of the absence of any means which permits a reasonably accurate estimation of the proportion of immature animals in the population and the suggested advanced age at which maturity occurs, it is not practical to attempt their construction.

A more elaborate statistical method for determination of death rates from capture-recapture data has been developed by LESLIE and CHITTY (50). Because of the numerous required assumptions previously stated, DAVIS and GOLLEY (19) question the advisability of applying complicated mathematical procedures to natural populations. As none of the aforementioned conditions are in conflict with the evidence on *B. subpalmata,* however, it seems advisable to attempt the application of this method.

I have utilized the "three-point" method of LESLIE and CHITTY (50) which permits an estimation of death rate from information at three sample periods of equal interval (in this case, four months) and allows for density fluctuations without becoming mathematically unwieldy. Incorporating the data from all marked populations survivorship (P) is expressed as

$$P = \frac{{}^{m}01\;{}^{s}2+{}^{u}1\;{}^{m}02}{{}^{m}12\,{}^{R}0}:$$

where ${}^{m}01$ equals the number of marked salamanders recaptured at the second sampling period; $^{m}02$, the marked animals from the first sample not recaptured until the third; $^{m}12$, animals marked in the first sample and recaptured at the second and third plus those marked at the second sample and recaptured at the third; $^{s}2$ equals the total marked specimens taken in the third sample; $^{u}1$, the unmarked animals taken in the second sample; and ^{R}o equals the total number of the first sample. Substituting values, $P = \frac{(8)\ (5) + (28)\ (2)}{(6)\ (74)} = 0.21$ per year and is treated as a constant for all age groups.

CAUSES OF MORTALITY

There seems to be little predation upon *B. subpalmata.* In the lower elevations birds and small mammals may take some toll, although no direct evidence is available. Of amphibians, *Rana pipiens* and *Eleutherodactylus* sp. occasionally occur in ponds and under rocks below 2,800 m. The known voracious and indiscriminate feeding habits of ranid and leptodactylid frogs suggest the possibility of these species as predators. The small ground snake, *Ninia oxynota,* has been captured in habitats on the Cerro that would indicate a possible predator relationship with *B. subpalmata,* although the two species have not been found together.

Throughout the vertical range of its distribution on the Cerro, *B. subpalmata* is found with two species of lizards. *Barisia monticola,* an anguid, commonly shares the same terrestrial microhabitat with this salamander, as does *Sceloporus malachiticus.* The latter is primarily insectivorous and is doubtful as a predator, although juveniles may compete for food items with *B. subpalmata.* A captive *Barisia monticola* ate an adult *B. subpalmata* within 24 hours after the lizard's capture.

It is possible that some diurnal bird species, such as *Turdus nigrescens,* the black robin, include salamanders in their diet. The complementary nature of activity cycles would permit only limited crepuscular predation. However, some salamanders can be found near the surface at margins of rocks and logs during the day. The possible nocturnal predators are not known.

Some suggestion as to the degree of predation upon *B. subpalmata* can be presented on the basis of the number found with recognizably regenerated or autotomized tails. Such records were not kept on all specimens, but an estimate of between 0.5 and 1.0 % is supported by the quadrat samples. This is much lower than the 7.6 % observed in *Ensatina* by STEBBINS (70).

On one occasion an attending female and egg mass disappeared from the nesting site. Because of previous observations the absence of the female was not surprising, but the complete absence of any remnants of the clutch which had been recently deposited, could only be accounted for by its transfer to another site or by complete destruction.

Parasites observed to infest *B. subpalmata* include nematode worms found in the digestive tract and mesenteries of 0.3 % (2 of 702) of the specimens examined. Acanthocephalan larvae occurred in the abdominal cavity of 0.4 % of this sample. No ectoparasites were observed and no microscopic studies were made of the tissues.

The likelihood of freezing or desiccation does not appear as a serious mortality factor. Temperatures below freezing are rare and localized in occurrence on the Cerro. Avoidance of these conditions can easily be accomplished by retreat below the surface. At lower elevations desiccation may be a relatively more serious threat during certain times of year, although subsurface retreat serves as an effective escape from the advancing dry season. On one occasion, May 14, 1962 a dead adult was found under a rock at the summit. It was not possible to explain the reason for death, nor to determine if its observed desiccated condition was the cause or result of death.

The impact of human activity upon populations of *B. subpalmata* is difficult to assess on a long range perspective. Lumbering and other practices which involve removal of much of the forest will be deleterious, especially when it is accompanied by the use of land for farming and grazing. However, the adaptability shown by *B. subpalmata* in utilizing man-made habitats is conspicuous. Road cuts, fills and talus slopes resulting from road-building activities are densely inhabited, especially in higher elevations. Debris, such as lumber and building materials, deteriorating where it has been abandoned at construction camps of more than twenty years ago has also been utilized by these salamanders. It is apparent that as man's activities change the environment the populations in the lower levels will be more drastically affected than those near the summit. These latter elevations are least suitable for human occupation or utilization and are most densely occupied by *B. subpalmata.*

INFLUENCE OF THE PHYSICAL ENVIRONMENT

To elucidate the influence of environmental factors on the Cerro de la Muerte upon the distribution and density patterns of *B. subpalmata,* laboratory as well as field studies were conducted on the moisture and thermal requirements of the species. All experimental animals were maintained at room temperatures of from 18 to 22° C for not more than a week prior to experimentation. The methods for measuring soil moisture and temperatures have been presented earlier. In addition, reliable body and ambient soil-air interface temperatures were obtained from some 25 specimens.

MOISTURE REQUIREMENTS

Prior to examination of environmental moisture relationships, the total moisture content of six specimens was determined. These animals were placed on super-saturated filter paper in closed gallon jars for 18 hours and then desiccated at 105° C for 48 hours. Table 9 gives pertinent records of hydrated weight, desiccated weight, and weight lost as percentage of initial weight. The smallest individual of the series (1.58 gms) is but 48.9 % of the largest (3.23 gms) although the difference in weight loss is only 1.1 % (79.7 and 80.8 % respectively). Range of weight loss is from 78.6 to 82.6 % (average 80.7 %).

TABLE 9

Total weights of B. subpalmata *before and after desiccation.*

Initial Wt. in Gms	Desiccated Wt. in Gms	Water Content as % of Total
1.58	0.32	79.7
1.67	0.29	82.6
1.86	0.33	82.2
2.13	0.42	80.3
2.95	0.63	78.6
3.23	0.62	80.8

CUNNINGHAM (17) reported almost the same percentage of weight loss for six desiccated *Batrachoseps pacificus.* In animals with initial weights from 0.8 to 3.20 gms, the proportion of water loss was from 79.7 to 81.5 % (80.6 % average). The smallest weighed only 25 % of the largest yet the difference in weight loss between these two was less than 2%. Water content was an essentially constant proportion of the total weight. I find no basis for his conclusion that smaller salamanders contain significantly more body water than larger ones.

Five experiments were conducted to establish the critical level of water loss in *B. subpalmata.* All 27 animals used in these experiments were prehydrated on super-saturated filter paper in closed gallon jars for 18 hours. A Thelco Precision Oven (Model 6) was heated to 40° C for 24 hours prior to experimentation to remove excess moisture from the cabinet and then allowed to stabilize at room temperature. The insulated cabinet walls permitted air temperatures to be maintained between 22 and 24° C at an uncontrolled relative humidity of from 50 to 58%. Before each weighing on a triple beam balance (Ohaus Centogram, Model 311) the specimen was "walked" over absorbent paper to remove excess body surface water. Care was taken to avoid any cloacal discharge. Weights were recorded immediately prior to experimentation and at intervals of about 45 to 60 minutes during the tests or at the onset of any observed stress. Six control specimens were maintained in covered moist chambers and subjected to otherwise identical conditions.

No behavior attributable to stress was observed in animals that had lost up to 32.3% of their initial body weight, but definite avoidance reactions were observed when the weight loss exceeded this value. None of the specimens survived water loss of greater than 41.2%. The latter value is consistent with that given by STEBBINS (70) for *Ensatina eschscholtzi,* but exceeds the average of 34.7% in *Batrachoseps pacificus* (CUNNINGHAM, 17). No weight loss or stress responses were noted among the control animals.

It was anticipated that because of surface-volume relationships smaller animals would suffer water loss more rapidly than larger ones. This phenomenon has been reported in amphibians by STEBBINS (70) and THORSEN (73). Of nine separately tested *B. subpalmata* weighing from 1.30 to 4.71 gms the loss rate per hour was found to be an almost consistent inverse proportion to initial weight. The results are presented in Table 10. Rates of loss are from 0.8 to 5.2% per hour, averaging 2.5%.

Certain behavior responses under stress of water loss were noted. In two instances adults autotomized the tail, but the actual water loss level at which this occurred was not observed. Coiling of individuals is also common once the stress threshold is reached. Animals subjected to dehyration in the same container persistently congregated in tight, ball-like masses, which effectively reduced the total exposed body surface area. Results from one experiment indicative of the effect of such behavior is given in Table 11. All six animals survived the 18 hour test. No isolated specimens ever survived this exposure period.

The smaller animals appear to gain somewhat more advantage from this cooperative behavior than larger ones. Those with initial weights of less than two grams had the hourly rate of loss reduced by at least 0.9% as compared to rates given in Table 10, and the average hourly rate for the two experimental groups was lowered from 2.5 to 1.1%, a difference of 1.4%. Similar behavior has been observed during aestivation of *Batrachoseps pacificus* (CUNNINGHAM, 17) and in experimental studies on *Aneides lugubris* by ROSENTHAL (63).

TABLE 10

Water loss rates of B. subpalmatas *demonstrating aggregation behavior. Experimental humidities between 50 and 58%.*

Initial Wt.	Desiccated Wt.	Time	% Lost	% Lost/Hr.
1.30	0.88	6.25	32.3	5.2
1.65	1.24	6.25	24.8	4.0
1.72	1.27	6.25	26.2	4.2
1.74	1.38	5.25	20.7	3.9
1.96	1.64	8.00	16.3	2.0
2.02	1.88	8.00	6.9	0.8
2.33	2.16	8.00	7.3	0.9
2.41	2.13	8.00	11.6	1.4
4.71	4.36	8.00	7.4	0.9

TABLE 11

Water loss rates of B. subpalmata *demonstrating aggregation behavior. Experimental conditions are the same as those stated in Table 10.*

Initial Wt.	Desiccated Wt.	% Water Lost of Initial Wt.	% Lost/Hr.
1.87	1.50	16.0	1.1
1.99	1.69	15.1	0.8
2.07	1.71	17.4	1.0
2.46	1.97	19.9	1.1
2.79	2.01	27.9	1.6
4.54	3.64	19.8	1.1

TABLE 12

Rehydration of dehydrated B. subpalmata *in two environments at 21 to 24° C.*

N°	Initial Wt.	Dehydrated Wt.	Environment	Wt. at 3 Hrs.	Deviation Init. Wt.	% Recov.
1	1.99	1.69	Submerged	2.30	+0.31	115.6
2	2.46	1.97	Submerged	2.88	+0.42	117.1
3	2.79	2.01	Submerged	2.67	—0.12	95.7
4	1.87	1.50	Moist Chamber	1.83	—0.04	97.9
5	2.07	1.71	Moist Chamber	1.96	—0.11	94.7
6	4.54	3.64	Moist Chamber	4.37	—0.17	96.2

Immediately following dehydration to levels of between 15.1 and 30.3% of initial body weight, a series of six specimens weighing from 1.50 to 3.64 gms were rehydrated. Three of these were submerged in water and the others were placed in covered ten cm culture dishes lined with saturated filter paper. The vessels were again maintained at temperatures of between 21 and 24° C. Pertinent measurements on water recovery are presented in Table 12.

The three submerged specimens averaged 109.4% of initial weight after three hours, while those in the moist chamber regained an average of 96.2%. Although the difference of the two averages is considerable (13.2%), there seems to be little ecological advantage gained by submergence as compared to saturated surfaces in rates of rehydration. All animals were well above the moisture stress limit of 32.3% within three hours and had essentially regained their initial weight. Although two submerged specimens weighed more than their initial weight at this time, it is significant to note that N° 3, in recovering 95.7%, was exceeded by two of the moist chamber specimens at 96.2 and 97.9%. At the end of five hours all specimens equaled or exceeded their initial weight.

Comparison of dehydration-rehydration rates of these same specimens cannot be made as aggregation behavior demonstrated during the former test resulted in modification of the weight loss rates. Even if only the moist chamber animals are considered, however, recovery rates are much greater than dehydration at the same temperatures, averaging 96.2% for the total test period or 32.1% per hour. This is six times greater than the most rapid hourly loss rate (5.2%) observed in separately dehydrated *B. subpalmata* and twelve times that of the average hourly loss rate of 2.5%. COHEN (16), using the same animals for dehydration and rehydration experiments, found *Aneides lugubris* to lose water 1.25 times faster than it gained, and *Ensatina eschscholtzi* to lose 4.66 times more rapidly. It may be that his differences are due in part to the fact that dehydration was carried out at 20° C and rehydration at 13° C.

Although the Cerro de la Muerte is subjected to intense rainfall during much of the year, *B. subpalmata* generally avoids drainage courses and inundated areas. On only six occasions were individuals seen in recently flooded microhabitats. Experiments were conducted to determine the length of time these animals can survive when submerged.

TABLE 13

Submergence tolerance of B. subpalmata *at temperatures of 22 to 23°C. CT equals capture threshold, PL equals physiological lethal.*

Standard Length (mm)	Sex	Wt. (gms)	CT (hrs)	PL (hrs)	Difference CT - PL (hrs)
37.5	♀	0.78	3.50	6.75	3.25
39.5	♂	1.01	3.75	10.25	6.50
40.0	♂	0.92	7.75	10.75	3.00
42.0	♀	1.18	6.50	7.75	1.25
42.5	♀	1.51	5.25	7.75	2.50
42.0	♂	1.26	—	10.25	—
45.0	♀	1.64	—	17.50	—
40.0	♀	1.67	—	< 11.00	—
51.5	♀	2.31	—	< 11.00	—
52.0	♂	1.99	—	< 11.00	—

Pint jars containing 300 ml of well water were allowed to stabilize for 24 hours at 22 to 23° C before experimentation. The water was not aerated during the experiments. Animals were maintained at room temperatures in containers partly filled with moss from the habitat site and tested within a week of capture. Table 13 includes the observations on ten experimental animals. The control group again comprised six specimens maintained in covered moist chambers during experimentation. Loss of righting ability, (capture threshold) either voluntarily or in response to strong pressure applied to the hind limbs, represents the limit beyond which escape is impossible. The physiological lethal point was taken as the cessation of capillary flow in the gular region. These criteria are essentially those used by STEBBINS (70). Time intervals are given to the nearest quarter hour of determination. Loss of righting ability occurred between 3.50 and 7.75 hours, with an average of 5.35. A much broader range of tolerance was demonstrated in physiological lethal points (6.75 to 17.50 hours; average, 10.14). Differences in periods between CT and PL averaged 3.30 hours (range 1.25 to 6.50 hours). No behavioral or physiological responses were observed in the control group. My information is inadequate to justify more than a general interpretation of these tolerances. It is evident, however, that at eight hours *B. subpalmata* has suffered irreversible lethal damage. STEBBINS (70) found an inverse correlation between size and tolerance to submergence in *Ensatina eschscholtzi*, which is not apparent in these experiments. The maximum time for loss of righting ability (equals "ecological limit" of STEBBINS) in three geographic races of *Ensatina* was 95 hours, while the greatest physiological tolerance (in unaerated water) was 98 hours.

The factors contributing to variations in habitat moisture have been treated in other sections. Twenty-six soil samples were taken from quadrats during the quarterly collections. The top centimeter of soil was removed from a nearly level site that was clear of debris or vegetation. Inundated or super-saturated sites were avoided. Laboratory methods used for determining the amount of moisture as percentage of dry weight were presented earlier. In several instances the values given here do not represent the actual moisture content of the microhabitats; however, most approximate it closely.

The percentage of soil moisture and relative (available) densities of *B. subpalmata* are given in Fig. 34. The influence of moisture upon the near surface presence of salamanders is obvious. Below 30% there is almost complete retreat to subsurface levels. In four cases where salamanders are shown as occurring at moisture levels below 20% (indicated by "L") the animals were not near the ground surface, but limited to and aggregated in localized sites of moisture under deeply imbedded rocks or decomposing logs. Thus, moisture contents of the soil samples given for these densities are not truly representative of the microhabitat. Above 30% a wide range of moisture conditions are tolerated and the optimum appears between 55 and 75%. Because of the influence it exerts on evaporation rates, temperature undoubtedly plays an important role in moisture requirements and contributes to the magnitude of this range. Below or above certain limits, however, available moisture is a critical factor in itself and cannot be ameliorated by temperature. The low surface density at 83% suggests avoidance of excessively wet conditions in the environment and, although an isolated record in measured soil moisture values, this conclusion is supported by field observations. ROSENTHAL (63) has experimentally determined that *Aneides lugubris* avoids excessively wet as well as very dry soil surface conditions at temperatures ranging from 2 to 29° C and that soil moisture is the dominant factor influencing habitat selection.

THERMAL REQUIREMENTS

Saturated chambers, each containing five animals (acclimated for seven days at 20 - 22° C) were placed in controlled temperature rooms at -4.0 (thermal variation ± 0.5)°, 4.0 (± 0.5)°, 27 (± 0.5)°, and 37 (± 1.0)° C. After exposure to the lowest temperature for a 75 minute period, the specimens survived from 2 to 48 hours before capillary circulation ceased entirely. None regained full locomotor capacity. At 4.0° C the animals became inactive, but suffered no deleterious effects after three weeks at this sustained temperature. After 50 hours at 27° C two were dead and a third died before 56 hours exposure. At this time the righting response of the two living salamanders was hindered and poorly coordinated. These did not survive 72 hours exposure. Within one hour all specimens in the 37° C room were dead. When placed in a plastic pan containing 0.5 cm depth of water preheated to 37° C, five other *B. subpalmata* instantly responded by violent thrashing of the body and tail, dying from thermal shock within 30 seconds.

ROSENTHAL (63) observed that *Aneides lugubris* did not survive more than 24 to 40 hours after exposure to -6° C for 45 to 60 minutes and concluded that temperatures much below freezing for more than 30 minutes are fatal. Thermal stress in *Aneides* was demonstrated at an average of 30.7° C for eight animals and the critical thermal maximum (CTM), indicated by the onset of spasms, was attained at above 33° C. In experiments with *Ensatina eschscholtzi* STEBBINS (70) obtained stress responses at 24 to 26° C and a CTM of 32 to 34° C. ZWEIFEL (82) and HUTCHINSON (44) have reported correlations of CTM and habitat differences in several species of salamanders. Of 20 plethodontid species and subspecies included in HUTCHINSON'S study, the averages of CTM'S for adults acclimated at 20 to 22° C were from 33.05 C (for *Gyrinophilus d. danielsi)* to 37.87° C (for *Manculus quadridigitatus)*. Congeneric species usually demonstrated similar CTM'S with the exception of *Desmognathus,* which exhibited significant differences between *D. quadramaculatus* (33.59° C) and *D. f. fuscus* (36.2° C).

Cloacal temperatures for 25 specimens of *B. subpalmata* obtained in the field closely approximated the soil-air interface temperatures of the microhabitat (Fig. 35). Body temperatures were taken immediately after uncovering the animal in its refuge. The hind foot was held and the thermometer inserted and read at its stabilization point within 15 to 30 seconds. If the specimen exhibited marked activity or the thermometer did not stabilize before 30 seconds, the reading was disregarded. The small size of juveniles did not permit body temperatures to be taken without measurable heat conduction from the observer. After removing moisture from the thermometer tip the soil-air interface was then measured by pressing the bulb into the substratum so that only the uppermost surface was exposed. Although various factors such as behavior, previous exposure, variations in conduction from the substrata and evaporation of body moisture can measurably influence body temperatures of amphibians, in plethodontid salamanders this is usually close to the temperature of the microhabitat. (Refer to BRATTSTROM, 11, for a general review). It has been concluded that the approximation of body and ambient temperatures is a result of the necessity for these terrestrial ectotherms to maintain body moisture by close contact with the wet substratum (BOGERT, 9; BRATTSTROM, 11; COHEN, 16).

Over 600 temperatures taken of microhabitats occupied by *B. subpalmata* have ranged from 2.8 to 23.8° C. Such extremes are attained only infrequently on the Cerro and although tolerant of lower thermal levels, at which it is not normally active, the species is rarely found at ambient temperatures in excess of 20° C. The range of body temperatures at which active animals have been observed is estimated from readings taken from the refugia at time of emergence. For 188 active animals my records range from 6.4 to 12.8° C (average 8.8 ± 0.6° C). BRATTSTROM (11) offers an extensive summary of "voluntary" thermal levels or microhabitat temperatures at which salamanders have been found. From over 555 records of 27 plethodontid species and subspecies he derives an average of 14.8° C (range - 2.0 to 26.2° C), which substantiates the conclusion of BOGERT (9) and STEBBINS (70) that a fairly wide thermal spectrum is tolerated. Of the plethodontids for which information is available, *B. subpalmata* exceeds the voluntary maximum reported for all species except *Manculus quadridigitatus* (26.2° C); only *Hydromantes platycephalus* and *Ensatina eschscholtzi*, at voluntary minima of -2.0 and + 1.0° C respectively, are lower. The range of observed "voluntary" temperatures (21.0° C) in *B. subpalmata* is greater than that known for any other salamander.

THE BIOLOGY OF *BOLITOGLOSSA SUBPALMATA* WITH REFERENCE TO EXTRATROPICAL PLETHODONTID SALAMANDERS

An evaluation of the biology and ecology of *B. subpalmata* can best be approached through comparison of data available on extratropical species. The more salient features presented in this study cannot, of course, be construed as applicable to all tropical salamanders, but certain conclusions offer valuable insight into the nature and dynamics of tropical populations.

The family Plethodontidae is found in both the eastern and western hemispheres, but in the Old World only two presumably relict species of the genus *Hydromantes* occur locally in the mountains and caves of southern Europe.

The family is distributed from southern Alaska to northwestern Mexico in a narrow belt along the western coast of North America. In the east its range continues from Nova Scotia to the northern half of Florida and broadly extends westward to cover most of the area between Texas and the Great Lakes region. Three isolated inland forms, one from Idaho and two from New Mexico, are the only plethodontids occurring in the subhumid continental region.

Absent from north central Mexico, plethodontids reappear in tropical lowland areas of the east and west coasts and along the southern margins of the Mexican Plateau. In the tropics the family occurs throughout Central America and two genera, *Bolitoglossa* and *Oedipina* range into northern South America, the former attaining its southernmost limits in Bolivia and along the Madeira and Amazon Rivers in Brazil. A summary of the New World distribution of the family is presented in Table 14.

Only three temperate zone species inhabit high montane regions. In New Mexico *Aneides hardii* is known from elevations of 2,700 to 2,800 m in the Sacramento Mountains and *Plethodon neomexicanus* from 2,670 m in the Jemez Mountains. *Hydromantes platycephalus* occurs between 1,540 and 3,260 m in the Sierra Nevada of California. All are members of genera found in lowland regions. All known tropical plethodontid genera are highland or montane forms; however, *Bolitoglossa, Oedipina* and *Parvimolge* include lowland species.

Extratropical plethodontids are adapted to a wide variety of habitats (BISHOP, 8; DUNN, 22, 23; GROBMAN, 32; HAIRSTON, 33; WAKE, 77). Of two subfamilies and sixteen or seventeen genera occurring in North American and Europe, aquatic, semi-aquatic and terrestrial habits are demonstrated in different

TABLE 14

Geographic Distribution of Plethodontid Genera in the New World.

GENUS	USA	México	British Honduras	Guatemala	Honduras	El Salvador	Nicaragua	Costa Rica	Panamá	Colombia	Venezuela	Peru	Ecuador	Brazil	Bolivia	Chile	Argentina
Desmognathus	X																
Leurognathus	X																
Phaeognathus	X																
Aneides	X	X															
Batrachoseps	X	X															
Ensatina	X	X															
Hemidactylium	X																
Plethodon	X																
Stereochilus	X																
Eurycea	X																
Gyrinophilus	X																
Haideotriton	X																
Hydromantes	X																
Manculus	X																
Pseudotriton	X																
Typholomolge	X																
Typhlotriton	X																
Bolitoglossa		X	X	X	X	X	X	X	X	X	X	X	X	X	X		
Chiropterotriton		X		X	X			X									
Oedipina			X	X		X	X	X	X	X							
Parvimolge		X						X									
Pseudoeurycea		X		X													
Lineatriton		X															
Thorius		X															
Haptoglossa (?)								X									

TABLE 15

Adult habitats of New World extratropical plethodontid genera.

Subfamily *Genus*	Pond	Stream	Stream Bank	Woodland	Talus, Rock Rubble	Arboreal
Desmognathinae						
Desmognathus		X	X	X		
Leurognathus	X	X				
Phaeognathus				X		
Plethodontinae						
Gyrinophilus		X	X			
Pseudotriton		X	X			
Stereochilus	X	X				
Eurycea	X	X	X	X		
Manculus	X			X		
Typhlotriton	X					
Haideotriton	X					
Typhlomolge	X					
Hemidactylium			X	X		
Plethodon			X	X	X	
Aneides				X	X	X
Ensatina				X		
Hydromantes				X	X	
Batrachoseps				X		

TABLE 16

Habit diversity of tropical genera of plethodontid salamanders.

Genus	Surface Dwelling	Burrowing	Saxicolous	Arboreal
Bolitoglossa	X	X	X	X
Chiropterotriton	X		X	X
Oedipina	X	X		
Parvimolge	X			
Pseudoeurycea	X			X
Lineatriton	X	X		
Thorius	X			

species known from lowland to subalpine regions. Nine genera include species with primarily aquatic or stream-dwelling adults (Table 15). The most extreme examples of aquatic life are two little known monotypic genera found in caves and artesian wells, the apparently paedomorphic *Haideotriton* and *Typhlomolge*. Several species of *Eurycea* also attain sexual maturity without metamorphosis. *Typhlotriton* is not known to depart from its underground aquatic habitat; while *Leurognathus* commonly occupies stream beds, seldom emerging beyond exposed rocks. *Stereochilus* requires slow-moving streams or ponds in low elevations. *Gyrinophilus* and *Pseudotriton* mark a transition between aquatic and terrestrial habitats. Adults of these two genera are stream and stream bank dwellers.

The widest habitat utilization is exhibited within the genera *Desmognathus* and *Eurycea*. Both include species of aquatic, stream bank or woodland habitats. *Manculus* is somewhat more terrestrial that most species of *Eurycea*. *Hemidactylium* is known from both stream banks and woodlands, while in *Plethodon*, unquestionably a terrestrial genus, only one species, *P. dunni*, is a stream bank form. *Batrachoseps, Ensatina* and *Phaeognathus* are woodland inhabitants with some propensity for burrowing. A special type of terrestrial habitat, the rocky slope, is utilized by some species of *Aneides, Hydromantes* and *Plethodon;* genera most typically from woodlands. It appears that the saxicolous habit has been derived from a more general terrestrial adaptation rather than through direct transition from an aquatic existence, as the only genera to include rock-dwelling species are those with terrestrial or woodland representatives.

Modern tropical plethodontids occupy a considerable range of habitat types, but no known tropical species can be ecologically equated with the aquatic or stream bank dwellers of temperate latitudes. It seems probable that since direct terrestrial development has emerged as a broad adaptation there has been little selective advantage in returning to water. Diversity has resulted from refinements, or extensions, of utilization of the terrestrial environment for which direct embryological development has been a preadaptation.

Most tropic salamanders are of a general terrestrial habit and are ground wanderers living under cover provided by litter. Nonetheless, within the seven recognized genera (omitting the enigmatic genus *Haptoglossa*), species manifest varying degrees of specialization. A summary of the more distinctive habits is given in Table 16. The restricted habits known for some genera, e.g. *Parvimolge, Thorius* and *Lineatriton* are undoubtedly a result of limited collecting and inadequate knowledge of tropical salamander ecology. *Oedipina* and *Lineatriton* are elongate, worm-like forms, well adapted to a subterranean existence. Talus slopes and rock rubble are especially frequented by *Chiropterotriton mosaueri* and *Bolitoglossa sooyorum.*

A unique community exists throughout much of the tropic zone which has provided amphibians with further ecological opportunity. The "aerial swamp" is a spectacular development of an extremely complex epiphyte community typical of humid tropical lowland and montane forests. Many thousands of epiphytic plants may conceal the major branches of a gigantic supporting tree. In species composition the "swamp" shows great variety, but the predominant plants are bromeliads or aroids having scoop-shaped leaves with bases that serve as reservoirs of rain water. The vertical extent of the "aerial swamp" usually depends upon the complexity of the forest and may extend between about 10 to 30 m in storied jungles. Most reports of arboreal habits in tropical salamanders include reference to bromeliad dwellers. Certain species, *Chiropterotriton picadoi, Chiropterotriton nasalis* and *Bolitoglossa alvaradoi,* are known only from this habitat.

The greatest generic diversity in habitat utilization is shown by *Chiropterotriton* and *Bolitoglossa.* Within the latter genus no species exceeds the valence of *Bolitoglossa subpalmata,* which retains the unspecialized terrestrial features of the family and exhibits a variety of habits (Table 16).

The extent to which the historical and present distribution of salamanders has been influenced by temperature and available moisture cannot be overestimated. Because of the intimate ecological relationships of the two factors it is desirable to consider them together. It is fortunate that an instrument such as the HOLDRIDGE (39) model is available by which this relationship can be empirically defined.

Consistent with my previous use of this system in treating of the local distribution of *Bolitoglossa subpalmata,* recent ecogeographic patterns of plethodontids and possibly all salamanders, can be measured in terms of biotemperature (discussed earlier) and the potential evapotranspiration rate. Potential evapotranspiration (PET) is the amount of water lost by evaporation and transpiration, presuming water to be continuously available. PET = (B) (K), where B is the mean annual biotemperature and K is a constant value of 58.93. To obtain the annual rate of PET, potential evapotranspiration is divided by the mean annual precipitation (HOLDRIDGE, 41, 42).

Superimposed on the base diagram of the Holdridge classification of Climatic Vegetation Formations presented in Fig. 36, is the general ecogeographic distribution of plethodontid salamanders. The latitudinal regions occupied by the family are Tropical, Low Subtropical, Warm Temperate and Cool Temperate. Equated with these regions are Tropical, Subtropical, Lower Montane and Montane altitudinal belts. Each latitudinal region, defined by biotemperature limits, includes the vegetation formations indicated by each of the hexagons within that latitude region and all of those at lower biotemperatures. For example, a total of 38 Tropical latitudinal formations are defined (counting seven each for Warm Temperate and Low Subtropical, which are separated by a critical temperature line of 17° C). The seven latitudinal regions include a total of 130 formations. Four regions and 30 formations are occupied by plethodontids, which are restricted to the Humid, Perhumid and Superhumid Humidity Provinces indicated at the base of Fig. 36. It would be a mistake to assume that a neat and clear-cut distributional picture shaped from the precise mold of Holdridge hexagons occurs in plethodontids. Salamanders and many other animals exhibit behavioral and physiological adaptations providing a means of escape from direct exposure to the physical environment. For example, hibernation, aestivation and migration are means of evading unfavorable extremes and permit the habitation of areas otherwise ecologically inaccesible.

In broad perspective the distribution of plethodontids is associated with two recognizable limits. Serious moisture restrictions are met when the PET ratio approximates 1.00; in other words, when PET exceeds the mean annual precipitation. Unquestionably the 1.00 moisture line is not a limiting factor for species capable of avoiding drought conditions. The dry forests of the Subhumid Province are marginal habitats which may be invaded by way of more humid environments. An excellent example of the occupation of marginal conditions is demonstrated by some salamanders of the warm temperate regions in the western United States, such as *Batrachoseps attenuatus, Aneides lugubris* and *Ensatina eschscholtzi,* that inhabit the oak forest community of California. Although actually a part of the Warm Temperate Dry Forest formation in the Subhumid Humidity Province, this community is occupied by these three species in localized areas where topography and drainage compensate for climatically inadequate moisture.

Few other salamanders inhabit the altitudes at which *B. subpalmata* is commonly found. *Pseudoeurycea rex* is abundant in the pine forest belt of Guatemala in the Tropical Montane altitudinal belt (the cool temperate climate of SCHMIDT, 65). In North America, *Aneides hardii* and *Hydromantes platycephalus* are high altitude relicts occurring in different localities at more than 2,700 m, but neither of these species occupies the subalpine belt. The upper thermal boundary of the Cool Temperate latitudinal region or the Montane altitudinal belt of 6° C biotemperature is probably near the minimum limit for salamanders. The summit area of the Cerro de la Muerte is climatically a Tropical Montane belt.

By using the 6° biotemperature as the minimum thermal limit for plethodontid distribution and applying the metric limits of altitudinal belts given by HOLDRIDGE (39, 42), the maximum elevation available for habitats would be about 4,000 m on the heat equator. Latitudinal increases would reduce this limit concomitant with lowering of the Montane-Subalpine boundary. There are no locality records by which to verify the occurrence of salamanders at this estimated maximum elevation in tropic zones, although Chirripó Grande (3,820 m), in the southern Talamancas of Costa Rica, offers an opportunity to test this idea.

Salamanders are not capable of prolonged exposure to subhumid conditions. As a rule, moisture and temperature operate together in limiting the distribution of terrestrial species. There are, however, certain conditions in which the two appear to operate independently. In thermal regions characteristically occupied by a species, moisture exerts a determining influence. For example, *Aneides lugubris* of the warm temperate region in California exhibits a close association with soil mosture and amount of annual precipitation, which ROSENTHAL (63) considers to be more important than temperature.

The humid provinces are subjected to thermal levels which may limit salamander distribution. *B. subpalmata* is essentially limited to Lower Montane and Montane thermal levels within the extensive Subtropical belt of comparable humidity. The present altitudinal distribution of tropical plethodontids is evidence of adaptation to thermal levels within the humid regions. Most tropical species are upland forms, reflecting their origins from the cool temperate Old Northern herpetofauna (SAVAGE, 64). Certain genera, most notably *Bolitoglossa* and *Oedipina,* have been successful in occupying the moist lowlands.

There are distinct differences in the types of effects of environmental temperatures upon *B. subpalmata.* Much of the work done on the critical thermal maxima (CTM) of extratropical salamanders has been reviewed by HUTCHINSON (44). However, evidence obtained during the present study indicates that the value of CTM may be of slight ecological importance. For example, the CTM for *B. subpalmata* lies somewhere near 37° C, yet the species cannot tolerate prolonged exposure to 27° C. Even more important is the thermal level limiting species distribution, which more accurately reflects the nature of adaptation. The wide range of voluntary temperatures recorded in the microhabitats (21° C) indicates a broad ecological tolerance in adults, but there are subtle, yet critical aspects to the picture. Microhabitats may have temperatures above 20° C at times, but *B. subpalmata* does not seem to be capable of sustained brooding behavior when subjected to prolonged exposure to such thermal levels. Moreover, the true ecological thermal maximum is probably near 16° C, above which eggs have not been observed to survive continued exposure.

Ecological thermal limits for *B. subpalmata* are, surprisingly, much below those of *Desmognathus fuscus,* whose eggs ZWEIFEL (82) has successfully incubated at 26° C. It should be noted, however, that the altitudinal distribution of *B. subpalmata* is generally equivalent in biotemperature to the cool temperate latitudinal region as compared to the warm temperate region occupied by *D. fuscus.* Therefore the tropical form has lower thermal limits than those tolerated by this extratropical species.

Plethodontid reproductive patterns can be classified into three basic types with only little overlap. In all but one genus the life cycles are notably consistent and can be categorized in the following manner. In Type I, the most primitive, the eggs are anchored in water and an aquatic larva possessing functional gills hatches. Upon transformation, the adult form is typically aquatic or semi-aquatic. Type II includes forms whose eggs are deposited on land and have larvae that migrate to water. After metamorphosis the adult emerges to occupy a terrestrial habitat. In Type III complete terrestrialism is exhibited. Unembryonated eggs are deposited on land and undergo direct development. The embryo hatches as a replica of the adult and loses the allantoic gills immediately upon hatching or soon afterwards. A summary of the occurrence of reproductive types in temperate zone genera is given in Table 17.

Probably the oldest and most generalized living plethodontid genus is *Desmognathus* (DUNN, 22; WAKE, 77) with about nine recognized species. In this group all of the patterns just described are represented. *D. quadramaculatus* is an aquatic form in all phases of its life cycle. Terrestrial eggs and adult stages are present in *D. fuscus,* but the larvae enter water upon hatching and do not emerge until metamorphosis. *D. wrighti* is terrestrial in all phases; the eggs undergoing direct development on land.

TABLE 17

A summary of the occurrence of reproductive types in temperate zone genera of plethodontids. The number of species (included in parenthesis) for each genus is essentially that of Wake *(77). See text for description of characters.*

Reproductive Types					
I		II		III	
Desmognathus	(7)	*Desmognathus*	(1)	*Desmognathus*	(1)
Leurognathus	(1)	*Hemidactylium*	(1)	*Aneides*	(5)
Stereochilus	(1)			*Batrachoseps*	(3)
Eurycea	(10)			*Ensatina*	(1)
Gyrinophilus	(3)			*Plethodon*	(17)
Typhlotriton	(1)			*Hydromantes*	(5)
Pseudotriton	(2)				
Manculus	(1)				
Total 8	(26)	Total 2	(2)	Total 6	(32)
Typhlomolge	(1) ?			*Phaeognathus*	(1) ?
Haideotriton	(1) ?				

TABLE 18

Temporal reproductive patterns of extratropical plethodontids based upon records of egg clutches. (Mostly from Bishop, *8 and* Stebbins, *69).*

Subfamily	Winter			Spring			Summer			Fall		
Genus	D	J	F	M	A	M	J	J	A	S	O	N
Desmognathinae												
Desmognathus							X	X	X	X	X	
Leurognathus						X	X	X	X			
Phaeognathus												
Plethodontinae												
Gyrinophilus									X		X	
Pseudotriton								X	X		X	X
Stereochilus		X		X								
Eurycea				X	X	X	X	X	X			
Manculus	X	X	X									
Typhlotriton												
Haideotriton												
Typhlomolge				X								
Hemidactylium						X						
Plethodon						X	X	X	X	X		X?
Aneides						X		X	X	X		
Ensatina					X	X	X	X	X	X		
Hydromantes										X	X	X
Batrachoseps	X	X		X							X	X

The pattern of occurrence of the three reproductive types is not indicative of evolutionary lines of the family in an orthogenetic sequence of aquatic, semi-aquatic, terrestrial habitats, but instead, adaptive parallelism. More genera are entirely aquatic than are terrestrial, but there are more terrestrial species.

Typhlomolge and possibly *Haideotriton* are paedomorphic, as are several species of *Eurycea.* Besides *Desmognathus fuscus,* the monotypic *Hemidactylium* and *Manculus* have amphibious life cycles. *Hemidactylium scutatum* has an aquatic larva. Adults of *Manculus quadridigitatus* are terrestrial and return to swampy areas to deposit eggs in water.

Complete escape from the necessity of reproductive migration to aquatic habitats has been attained by several extratropical genera including one species of *Desmognathus. Phaeognathus hubrichti* is not yet known in all phases of its life cycle, but the adult is a fossorial woodland form, which strongly suggest completely terrestrial adaptations. *Plethodon* includes seventeen species, all of which have terrestrial life cycles. *Ensatina, Batrachoseps* and *Aneides* also have the free-living larval stage completely suppressed.

Reports of ovoviviparity in plethodontids have persisted through many years. Two classic studies on amphibian biology (DUNN, 22; NOBLE, 53) have undoubtedly contributed much to the perpetuation of erroneus observations. Berg's (1896) report of live birth in *Hydromantes italicus* is cited by DUNN (22, p. 348). NOBLE is probably referring to the same species when he states it "retains the eggs in the oviduct and gives birth to fully transformed young" (53, p. 59). GORMAN (31) incorporated a literature review on the life history of *Hydromantes* and implied that there is no adequate proof of ovoviviparity. Only terrestrial (Type III) plethodontids have become successfully established in the tropics. No other salamander family is known south of the Mexican Plateau. Although information on life histories of the seven tropical genera is meager, all known species are terrestrial (or arboreal) as adults and the evidence available at present strongly suggests that the suppressed larval stage is typical of all tropical species. NOBLE (53) regarded the tropical genus *Oedipus* as ovoviviparous. The source of his statement is probably Posada (1909), cited in DUNN (22), who reported this phenomenon in *Bolitoglossa* (= *Oedipus*) *adspersa.* STEBBINS and HENDRICKSON (71) have observed this species in the field and question Posada's observations. BRAME and WAKE (10) have made a comprehensive study of South American salamanders without finding any evidence of viviparity or ovoviviparity.

If the degree of adaptive radiation is a measure of evolutionary success in a group of organisms, then the terrestrial plethodontidae have been the most successful members of the family. Of the extratropical genera, the genus *Plethodon* has differentiated into more species and occupies a greater geographic area than any other. What special advantage may be gained by a salamander occupying a terrestrial habitat is difficult to define precisely but on the basis of comparative survivorship rates in *Desmognathus,* ORGAN (56) has concluded that it may be the escape from higher mortality factors present in aquatic habitats, particularly during embryogenesis and early larval life.

In studies of salamander ecology, various criteria of reproductive periods have been adopted; *e.g.,* large ovarian eggs and gravid appearance of females, deposition of spermatophores, swollen cloacal lips, etc. I have used reports of oviposition as an indication of the reproductive period because this character offers an undeniable and consistent advantage. It is a feature easily recognizable and is unlikely to be omitted an any life history study. However, the actual period of deposition is not necessarily equated with that of finding clutches in the field. Egg laying is adaptively timed to provide an adequate interval for development and hatching and therefore terminates before the onset of seasonally unfavorable environmental conditions. The finding of eggs in the later stages of embryogenesis cannot be construed to indicate the "reproductive" period of adults.

If available data on oviposition are classified according to genera and time of the year, several features of reproductive periods of extratropical plethodontids become apparent. The member genera have reproductive periods that extend from only a few weeks to a substantial part of the year. *Ensatina* and *Eurycea,* for example, have a period of six months during which egg masses have been found in the field, usually through spring and summer. *Desmognathus, Aneides* and *Plethodon* all begin reproduction in early summer and continue well into the fall. In California, the eggs of *Hydromantes* are deposited only during the fall (GORMAN, 31). Only three genera have been observed to include winter months in the period of egg deposition. *Batrachoseps* is reported by various workers to nest from October through March. *Stereochilus marginatus* is known to brood its eggs in January and March; the latter month may represent the termination of its cycle (SCHWARTZ and ETHERIDGE, 66). Eggs of *Manculus quadridigitatus* have been found during December, January and February.

The periods of reproduction reported for plethodontid genera are given in Table 18. By treating temporal patterns at the generic level recognition of the broader cyclic characteristics is permitted at the expense of measuring specific ones.

The subfamily Plethodontinae is the most diversified of the Plethodontidae and includes about 20 genera, two-thirds of which are extratropical. Information available on periods of oviposition for genera in this subfamiy shows that temporal occurrence of egg laying cycles extends over the range of the entire family. Certain species demonstrate seasonal variation of cycles in different local populations correlating with periods of most favorable environmental conditions. One species of *Plethodon (P. glutinosus)* lays its eggs from May through September, but oviposition probably does not continue for more than two months in most local populations. HIGHTON (37) reported that in Florida the species deposits eggs during August and September, while in Maryland and Pennsylvania deposition probably occurs in late spring. *Ensatina* lays its eggs during a later period in northwest Oregon than it does in California (GNAEDINGER and REED, 26). It seems reasonable to predict that the reproductive period could be prolonged if environmental limits were ameliorated. Except for isolated collecting records, information on temporal reproductive patterns in tropical salamanders other than *Bolitoglossa subpalmata* is lacking, but in view of the adaptive range evidenced by temperate zone genera, it is not at all surprising that this species is acyclic.

KLOPFER (48), citing data from Skutch (1954, *et seq.*) makes particular note that breeding cycles in related species of tropical birds occupying the same habitats are staggered, thus reducing the intensity of competition for food and nest sites. Obviously, alternation of reproductive periods permits most effective interspecific use of any environment, tropical or not, as shown by extratropical plethodontids at both the generic and species level. It is not yet known if cyclic and staggered reproduction occurs in tropical salamanders.

Klopfer's statement, though valid, tends to obscure the intraspecific advantages of acyclic reproduction. By extending the period of use of available nesting sites, the degree to which reproductive potential or population densitites are limited by the number of sites is reduced as compared to populations having strongly phased reproductive cycles. Further advantage is gained in that most unfavorable physical changes in the environment are of short-term duration and would not affect an acyclic population to the same degree as if encroaching at a period when a synchronized reproductive phase is in progress.

Formation of testicular lobes in plethodontid salamanders has been attributed by HUMPHREY (43) to the following conditions: slow forward movement of the spermatogenic wave; delayed regeneration of emptied lobules; and a time interval following which the long postponed regeneration brings into existence a new lobe. I agree with his conclusions in spite of the fact that they are based upon the premise: "the urodele male it will be recalled completes but one sexual cycle annually". There may be a great deal of difference in relative rates of tissue reactivation in *Desmognathus fuscus* and *B. subpalmata,* but a slow spermatogenic wave and delayed regeneration of the secondary germinal cord does not inhibit continuous sperm production.

That the environment is not a universal causative agent of lobed testes in salamanders is established by the absence of lobing in the widely distributed temperate zone *Plethodon glutinosus.* The slow movement of the spermatogenic wave may be continuous and the period of time between degeneration of spent lobules and reactivation of this spent tissue may be relatively short, permitting regeneration of part of the lobe before the remaining portion has been completely exhausted of sperm cells. Testicular lobing is known for several members of the subfamilies Desmognathinae and Plethodontinae and probably became genetically fixed in their early history. This would explain most simply the occurrence of lobed testes in both extratropical and tropical forms. The alternative is to conceive of this character as having originated separately and independently in several other tropical species closely related to *B. subpalmata,* such as *B. adspersa, B. cerroensis* and *B. sooyorum,* which, on the best morphological and geographical evidence, are tropical upland forms of the Central American complex of the Old Northern herpetofauna (SAVAGE, 64). On the basis of observations on *B. subpalmata,* a reduction in the number of testicular lobes in tropical species may be a prevalent character. The continuous regeneration of germ cord cells could contribute to an increase in size and consequently a reduced number of lobes.

Biennial cycles of reproduction in female plethodontids are reported for five species of *Desmognathus* (ORGAN, 56) and is possibly a common feature in other temperate genera. The intensity of the brooding habit and a period of winter inactivity impose limitations of food gathering and yolk development which, according to that author, prohibit more frequent egg production. If the environment so rigidly influences female reproductive cycles in the Balsam Mountains of Virginia as indicated in Organ's study, it should be anticipated that in equable tropic environments no restrictions would be imposed. Moreover, potentially higher productivity levels in the tropics should provide optimum conditions for increased fecundity as it has for sperm viability. Nevertheless, it appears that *B. subpa mata* females have approximately biennial cycles of oviposition.

Adult *B. subpalmata* males are capable of reproduction throughout the year. Apparently the primary germinal tissue does not mature until the average age of six years. After a lobule is spent, about two years is required for reactivation of this tissue. It is difficult to picture the origin of a two year periodicity as being caused by an environmental influence, and if it is a temporal expression nowhere would it be more likely to be modified than in the tropics. The major significance of a biennial cycle lies in the time required for the maturation of tissues. Generally, females do not appear to reach maturity until about the eleventh year, possibly because of a metabolic level lower than that of males (WILLS, 81) and greater nutritive requirements for yolk storage. Even with sustained feeding during brooding, and the absence of any prolonged dormant period, an approximately two year egg laying interval is demonstrated. In view of the apparent absence of environmental influences it seems likely that the temporal patterns of maturation exhibited in *B. subpalmata* originated in the cool temperate antecedents of the species and have proved non-adaptive in the tropics. The lack of any necessity for extended hibernation or aestivation, and an essentially continuous availability of food, has enabled the population to prolong breeding activities throughout the year. Continuous reproduction in anurans has been reported in nine species from the Argentinian Chaco by CEI (14); in seven species from Singapore by BERRY (7); *Bufo melanostictus* from Java by CHURCH (15) and *Rana erythraea* from Sarawak (INGER and GREENBERG, 45).

For over fifty years the significance of the persistent incubation habit so typical of plethodontid salamanders has been the source of speculation and controversy. Several functions have been assigned this behavior, well known to be a necessity for sustained development of the embryos. Active defense of the eggs by aggresive lunging and biting has been observed in *Aneides aeneus* (GORDON, 28) and in *Plethodon cinereus* by HIGHTON and SAVAGE (38) as well as BACHMANN (3). PIERSOL (58) and NOBLE (53) suggested that the damp body of the parent assures the eggs of sufficient moisture. HIGHTON and SAVAGE (38) also observed that presence of the female promotes growth and yolk utilization. PIERSOL'S (58) hypothesis that dermal secretions of attending adults reduces eggs mortality by inhibiting mold infestations was perpetuated by NOBLE (53) and has been the basis of some commentary by almost every subsequent paper treating reproductive behavior of this family.

DUNN (23) and NOBLE (52) have effectively argued for the aquatic origin of the Plethodontidae and NOBLE (53) has described brooding behavior in some of the more primitive contemporary forms. It seems paradoxical to consider that antibiotic secretions are likely to have originated in conditions where they are subject to rapid dilution and removal in flowing water. Neither GORDON (28) nor HIGHTON and SAVAGE (38) found positive evidence of antibiosis. DANIEL and SIMPSON (18) reported negative results in antibiosis experiments with three species of salamanders, although none were plethodontids or terrestrial egg brooders. There is little doubt that the brooding adult plays an active role in survival of the eggs of *B. subpalmata.* No eggs were observed to continue development more than two weeks after being abandoned. In all of my observations attack by mold occurred only after the embryo appeared dead and the processes of decomposition were initated.

Another possible function has been almost entirely neglected. SMITH (67) noted that the aquatic eggs of *Cryptobranchus* would deteriorate *in vitro* unless placed in conditions where they were gently agitated by water currents. PIERSOL (58) postulated that manipulation of the eggs by an attending adult likely prevented malforming adhesions in the developing embryo. The observed manipulation of eggs by *B. subpalmata* indicates that some mechanical function may be of critical importance. A reexamination of the reproductive behavior of several plethodontid species further suggests that this kinetic function may be more significant than previously recognized.

Desmognathus quadramaculatus and *D. monticola* affix their individually stalked eggs to the nesting cavity roof. ORGAN (56) has reported these eggs being subjected to pendulous motion by water currents and activity of the attending female. The egg clutches of *Gyrinophilus danielsi* are deposited in streams and fastened to the substratum by a pedicel; thus being lightly agitated by minor variations in water turbulence. *Plethodon cinereus* has been observed to brood its eggs in such a manner that the entire clutch may twist about the single pedicel as the female moves beneath it (HIGHTON and SAVAGE, 38). In *B. subpalmata* the observed manipulation and rotation of the clutch is analagous. The importance of the brooding habit may lie in a dual or multipurpose relationship, one of which may be the necessity of frequent kinetic assistance.

The nature of the brooding instinct appears highly variable in plethodontids. Females of five species of *Desmognathus* were never observed to leave their eggs, even for feeding (ORGAN, 56); GORDON (28) reports a similar situation for *Aneides aeneus.* Intermittent wanderings have been noted among brooding females of *Aneides hardii* (JOHNSTON and SCHAD, 46), and *Ensatina eschscholtzi* (STEBBINS, 70). There have been no previous reports of males brooding the eggs, as has been found in *B. subpalmata,* but STEBBINS (69) speculated that both sexes of *Aneides lugubris* may attend the clutch.

Calculated rates of growth in the present study are conspicuously lower than those known for other Plethodontidae, although the period of field work offers a limited basis for extensive comparison. If HIGHTON's (36) figures are converted to approximate annual rates, four marked and recaptured specimens of *Plethodon glutinosus* grew between 6 and 21 mm per year, the smallest having the most rapid growth. He also noted that hatchlings of 12 to 15 mm almost double their length in the first eight months and may exceed 30 mm within the year. In northern populations, *P. glutinosus* grows more slowly, but attains a larger size than those in Florida (HIGHTON, 37). *Batrachoseps attenuatus* demonstrates a slower growth rate above 35 mm than in smaller individuals (HENDRICKSON, 35). *Ensatina* hatches at about 20 mm standard length and may grow to 35 mm by its second spring at approximately 18 months of age (STEBBINS, 70). *Bolitoglossa subpalmata,* emerging at 10 mm, and requiring an estimated two years to double this length, is not greatly different from the latter species in its early proportionate growth.

Maturity is attained at a fairly uniform age in temperate zone plethodontids. *Plethodon glutinosus* is usually capable of breeding at the third year in Florida and at five years in the northern part of its range (HIGHTON, 37); *Ensatina* usually in the third, although some may be delayed until the fourth year (STEBBINS, 70). According to POPE and POPE (61), *Plethodon ouachitae* matures in the fourth season, and *P. yonahlosee* probably requires the same time (POPE, 59). The western species, *Batrachoseps attenuatus,* is estimated to require two to four years before reaching reproductive capacity (HENDRICKSON, 35). In some species of *Desmognathus* the males mature in the fourth year, while females are delayed until the fifth (ORGAN, 56). The smallest male *B. subpalmata* producing sperm is estimated to be four years of age and egg laying in females probably occurs no earlier than the tenth year. With variations in growth and the absence of seasonality, maturity may occur earlier.

Maximum age estimates of other plethodontids are almost half that computed for the species under study. HENDRICKSON (35) gives a maximum age of ten years in *Batrachoseps attenuatus* and STEBBINS (70), eight and one-half years for *Ensatina.* I can offer no adequate explanation for the marked retardation in growth and maturity in *B. subpalmata.* One possible factor may be low activity levels of the populations which could be reflected in reduced growth rates and retarded maturity. Unfortunately, there is no quantitative data on activity levels for any other species of salamander. HIGHTON (37) has suggested that the reduced growth rate of *Plethodon glutinosus* in the northern United States is related to the decreased activity imposed by hibernation.

It is generally recognized that tropical biotic communities include a greater number of genera with fewer individuals of each member species than those of temperate regions. Nonetheless, the densities of *B. subpalmata* on the Cerro de la Muerte are rarely exceeded by any species of plethodontid in the temperate zone. Several features of the ecology of this tropical salamander elucidated by the present study may help to explain the observed population magnitudes: (1) high productivity levels in the tropical environment, (2) broad ecological use of the habitat, (3) the possibility of relatively low energy demands by the species, (4) acyclic reproduction, and (5) lack of territorial requirements. The estimated densities of the Cerro populations markedly exceed those of all other terrestrial plethodontids except those observed by ANDERSON (2) in the

San Francisco Bay island populations of *Batrachoseps attenuatus* and *Aneides lugubris.* Classically simplified island ecosystems which may include large numbers of individuals of few species are not homologous to the complex tropical habitat of the Cerro de la Muerte. Any explanation of the high density levels attained by *B. subpalmata* is probably of a different character. On the basis of the above enumerated features, it seems that this species is remarkably successful in an environment which provides a high density-independent, physical carrying capacity.

Attempts to estimate survivorship by different methods have produced widely variable results. In computing constant rates, based on capture-recapture data, the results are influenced by several factors: the high densities of salamander populations on the Cerro; great fluctuation in the number of available animals; and the small proportion of the total which are active during any given period. The values of $P = 0.09$ and 0.21 derived by the simple proportional method and the LESLIE and CHITTY (50) three-point system, respectively, are probably unrealistically low, being based upon the assumption that an animal captured on one occasion is equally at risk of capture on the next. As this is but the first attempt to apply the latter procedure to salamander populations, its reliability under such conditions has yet to be tested.

ORGAN'S (56) procedures for determining survivorship produce significantly higher results. Based upon single capture data, age specific survivorship rates of 0.29 and 0.65, when considered in relationship to an estimated partial potential reproductive capacity of 0.58, is not consistent with the concept, "the greater the ecological mortality, the greater the reproductive potential of the species..." (ALLEE *et al.,* 1). *B. subpalmata* has a higher average number of eggs per clutch than most plethodontid species known, according to comparative data given by JOHNSTON and SHAD (46); a characteristic of species having high population replacement and short life expectancy. The estimated individual longevity of adults is unusually high. These factors would indicate that eggs and young have but little chance for survival. The absence of any homing behavior or strong fidelity on the part of brooding adults, as compared to other species, infers a higher mortality in eggs than possibly any other phase of the life cycle. As no information is available on the survival of eggs, the estimated reproductive potential is definitely excessive. If, as assumed, the population is neither increasing nor decreasing, the balance would be best indicated by a lower realized reproductive performance and an annual survivorship rate of between the calculated minimum and maximum ($P = 0.09$ and 0.65).

The only quantitative information on survivorship in salamander populations are those of ORGAN (56) for five species of *Desmognathus.* No general comparison can be made with his computed life table values, as there are significant features in the life cycle of desmognathines which contribute to a differential survival in the sexes. These factors, specifically considered earlier, are not characteristic of *B. subpalmata.* Certain of Organ's data offer a means by which the sexual survivorship differential can be eliminated and mortality factors more or less equated. By omitting brooding females and assuming that males and non-brooding females of *Desmognathus* represent the conditions obtaining in *B. subpalmata,* a reasonable comparison can be made. ORGAN (56) has determined annual survivorship rates for two age periods, "early" and "later" life, based upon testicular lobes and year classes. Although the age periods, maturity and year classes are not the same as in *Desmognathus,* the lobe formation period, two years, approximates that of *B. subpalmata* and the values are derived by the same procedures (Table 19). It should be carefully noted that "later age" of *Desmognathus* is estimated to be younger than the "early age" of *B. subpalmata* (seven to eight and nine to ten years, respectively). Therefore the value of 0.65 for "early age" *B. subpalmata* is evidence of greater survivorship than of any species of *Desmognathus* at "later age" and is consistent with Organ's conclusion that survivorship values and degree of terrestrialism in salamanders are correlated.

TABLE 19

Mean annual survivorship rates in age periods of some plethodontid salamanders. See text for explanation of age categories.

Species	Early Age	Later Age
D. *quadramaculatus*	0.43	0.38
D. *monticola*	0.51	0.53
D. *fuscus*	0.62	0.40
D. *ochrophaeus carolinensis*	0.74	0.57
D. *wrighti*	0.91	0.29
B. *subpalmata*	0.65	0.29

In conclusion, it may be re-emphasized that several features of the tropical salamander, *B. subpalmata,* are distinct and considerably amplify our previously existing knowledge of amphibian biology. In the moist tropics, temperature is recognized as a critical limiting factor in geographic distribution. Under the influence of an equable environment, not only does *B. subpalmata* demonstrate year round activity, but acyclic reproduction. Both sexes are known to attend the egg clutches actively and persistently, although the intensity of the brooding instinct as well as of homing behavior is low. The growth rate appears to be essentially uniform throughout the life history of an individual and no sexual differences are exhibited. In comparison to extratropical plethodontids the calculated growth rate is the lowest known, but the maximum computed age is almost twice that of any other member of the family and maturity is concomitantly delayed. Unusually high population densities and survivorship rates among adults are also indicated in the Cerro populations.

SUMMARY

An intensive field study was conducted on the montane tropical salamander, *Bolitoglossa subpalmata* (Boulenger) in the Cordillera de Talamanca of Costa Rica. Information was obtained on over 4,000 specimens from quadrats, random samples and from six marked populations. Measurements of the physical environment and laboratory experiments supplemented the field data. The results and conclusions of the study are as follows:

1. The vertical distribution of the species extends from approximately 1,375 m to over 3,200 m; however, below 2,400 m the distribution is localized and densities are very low. Tropical vegetation formations characteristically inhabited by *B. subpalmata* include the Tropical Lower Montane Wet Forest and the Tropical Montane Rain Forest. Clay crevices, depressions under logs, rocks and moss, as well as the arboreal habitat, are utilized by this nocturnal salamander on the Cerro de la Muerte. Although the major distribution pattern of the species seems to be determined by thermal limits, the type of habitat selected is influenced by temperature and moisture in both elevational and seasonal occurrence.

2. Microscope slides of gonadal tissue show continuous sperm production in adult males. The lobular formation of testes is similar to that which has been described for *Desmognathus*. Females probably require about two years to complete a cycle of oviposition, although at any time some individuals in the population are in a reproductive stage. Convoluted oviducts are retained throughout the life of the mature female.

3. *B. subpalmata* usually nests under rocks and debris in well protected sites. The selected sites permit avoidance of both excessively wet or dry conditions and have a stability of temperatures between about 10 to 16° C, which appears to be the optimal range (the upper level may be ecologically critical). Usually the size of a nesting site restricts its occupation to but one clutch; however, up to three egg masses with their attending adults have been found in a single "nursery".

4. Unstalked eggs are deposited singly or in a series of two to four. If not situated in a grape-like cluster at the time of laying, the ovipositing female may actively gather them together. The clutch averages 23 eggs and is not fixed to any object. The eggs are about 5 mm in diameter and cohere by the outer membranes. Persistent, but not constant, attendance of an adult is required for sustained development. Both males and females have been observed to brood the clutches.

5. After the estimated four to five month period required for development, a completely transformed young ruptures the two enclosing membranes by violent body contortions. Shortly after emergence it retreats to protective cover. For the first two years growth is relatively rapid, probably about 5 mm per year, after which it reduces to a fairly constant calculated average of approximately 3 mm per year. No sexual differences in growth rates are known.

6. The species is active throughout much of the night, however, the pat-

terns of activity are variable and influenced by temperature and, more frequently, by humidity. Maximum activity levels appear at temperatures above 6° C and relative humidities of more than 80%, and are somewhat reduced at times of actual precipitation. Probably between 10 and 25% of the near-surface population is active during any given night.

7. Vagility in *B. subpalmata* is limited and individuals utilize a definite home range. No statistically significant differences were found in the movements of males, females and juveniles either in distance or in frequencies. The average home range area for all of these groups is 44 sq. m. There is no evidence of any homing behavior in displaced individuals.

8. Aggregations appear to be a response to unfavorable environmental conditions and are not related to reproductive behavior. Avoidance of extremely dry or wet conditions results in congregation at the most favorable habitat sites.

9. Densities of *B. subpalmata* on the Cerro attain striking proportions and are locally controlled by density-independent factors. Population densities are correlated with elevation; the greatest densities are found near the summit and in this area may exceed 9,000 animals per hectare (3,690 per acre). Both local and seasonal changes in moisture influence the occurrence of animals at the surface and during the dry periods they retreat to sub-surface cover.

10. Age class estimates of populations, admittedly speculative, are based on the measured hatchling size and calculated growth rates. The maximum age attained is about 18 years. Sexual maturity is apparently attained by males in the sixth year although it is not until the twelfth year that most females have deposited eggs. Males probably not only mature more rapidly, but reach senility earlier than females. The expected one-to-one sex ratio occurs at all seasons and throughout all age groups except the oldest, in which females notably exceed males.

11. Observations of numbers of egg clutches and spent females are used for determining the estimated annual partial potential reproductive capacity of 58%.

12. Survivorship and mortality estimates, computed by different mathematical procedures, are variable to a degree that casts serious doubts upon the application of most of these methods to salamander populations. The fluctuation of population densities, extensive use of the habitat, and low activity levels contribute to problems in using recapture records. The consistent absence of immature animals in the samples presents almost insurmountable problems in using single capture data.

13. The best available annual survivorship estimates are between 0.29 and 0.65, decreasing with age. It has not been feasible to construct life tables or survivorship curves. The potentially high reproductive capacity and low observed mortality factors acting upon adults suggest a high juvenile and egg clutch mortality. A high mortality rate of eggs is further indicated by the absence of strong attendance fidelity on the part of adults and lack of homing behavior in *B. subpalmata.*

14. Moisture requirements of the species are similar to several extra-

tropical plethodontids. The total body moisture averages about 80% of body weight. No behavioral stress is noted in animals losing up to 32.3% of initial body weight, although none survived a loss of more than 41.2%. Rates of water loss averaged 2.5% per hour, but are somewhat higher in smaller animals. Loss rates in all individuals are reduced by aggregation behavior. Rehydration is accomplished up to six times more rapidly than dehydration at the same temperatures. Rates of water resorption in saturated conditions are less than that of an individual when submerged, but the latter environment offers little, if any, ecological advantage.

15. Periods at which the loss of righting ability occurred under submerged conditions ranged from 3.50 to 7.75 hours (average 5.35), and cessation of capillary circulation was noted at from 6.75 to 17.50 hours (average 10.14). The average difference between these periods was 3.30 hours.

16. Soil moisture exerts a great influence on surface occupation of the habitat areas. Salamanders are virtually absent at less than 30%, the optimum range being between 55 and 75%.

17. Adult *B. subpalmata* can survive prolonged exposure to temperatures between 4 and 24° C. At below freezing temperatures (— 4.0 C) death usually results after less than two hours exposure. Temperatures of 27° C are lethal after 72 hours, while lethal thermal shock is almost immediate at 37° C.

18. Ecological thermal limits are probably at a sustained level of about 16° C, above which no eggs were laid. The critical thermal maximum (CTM) of approximately 37° C is here considered as a physiological, rather than an ecological, maximum and not the limit of tolerance at the most susceptible stage of the life cycle.

19. Body temperatures show little variation from those of the microhabitat. The range of voluntarily tolerated temperatures of from 2.8 to 23.8° C (a difference of 21°) is greater than that reported for any other plethodontid species.

20. Temperate zone plethodontids occupy a wider variety of habitats than those in the tropics. None of the latter are known to be aquatic. Probably there has been little selective advantage in returning to water after the evolution of direct development. *B. subpalmata* is not exceeded in its habitat utilization by any single species in the family.

21. Both tropical and extratropical plethodontids are generally absent from areas where annual precipitation is less than potential evapotranspiration, except where these are modulated by local conditions. Minimum temperature limits are probably close to the 6° C biotemperature level. Altitudinal patterns of distribution in various tropical species indicate adaptations to different thermal levels.

22. Three types of reproductive patterns are exhibited in plethodontid genera. *Desmognathus* includes species in all of these patterns. It is very probable that all tropical species, like *B. subpalmata,* have direct development.

23. Extratropical plethodontids have notably staggered breeding periods, both as populations and as distinct species. Acyclic reproduction in *B. sub-*

palmata maximizes use of available nesting sites and permits evasion of short-term unfavorable physical changes in the environment at the population level.

24. Testicular lobing apparently is a manifestation of limits imposed by metabolic capacities of the primordial germ tissue and is not correlated with environmental periodicity. Biennial oviposition is limited by similar intrinsic conditions.

25. It is suggested that of the probable multiple functions of brooding behavior, manipulation of the eggs by the adult satisfies a vital kinetic requirement that prevents developmental adhesions, thus being in part, analagous to an amnionic function.

RESUMEN

Se presentan los resultados de un estudio de la salamandra montícola tropical *Bolitoglossa subpalmata* (Boulenger) en la Cordillera de Talamanca, el cual abarcó más de 4.000 ejemplares obtenidos en cuadrículas, por muestreo al azar, y de seis poblaciones marcadas. Medidas del ambiente físico y experimentos de laboratorio sirvieron de suplemento a los datos de campo. Los resultados y conclusiones del estudio son los siguientes:

1. La distribución vertical de la especie va desde unos 1.375 m hasta más de 3.200 m; sin embargo, bajo los 2.400 m la distribución es irregular y las densidades muy bajas. Las formaciones de vegetación tropical habitadas característicamente por *B. subpalmata* comprenden el Bosque Húmedo Montano Bajo y el Bosque Pluvial Montano. Esta salamandra nocturna utiliza en el Cerro de la Muerte grietas en el barro, depresiones bajo troncos, piedras y musgo, así como el habitat arbóreo. Aunque la distribución de la especie parece determinada principalmente por límites térmicos, el tipo de habitat escogido es influido por la temperatura y la humedad tanto en relación a la altitud como con las variaciones estacionales.

2. En cortes microscópicos de tejido de las gónadas se observa producción continua de espermios en los machos adultos. La conformación lobular de los testículos es semejante a la descrita en *Desmognathus.* Las hembras parecen necesitar dos años para completar un ciclo de oviposición, aunque en cualquier momento algunos individuos de la población están en una etapa reproductiva. Las hembras maduras mantienen oviductos convolutos durante toda su vida.

3. *Bolitoglossa subpalmata* generalmente anida bajo rocas y escombros en sitios bien protegidos, que permiten evitar condiciones excesivamente húmedas o secas, y que tienen temperaturas estables entre 10 y 16º C; este parece ser el ámbito óptimo de variación (los niveles superiores pueden ser críticos ecológicamente). Generalmente el tamaño del sitio impide que haya más de una nidada; pero hasta tres masas de huevos con sus guardianes adultos se han hallado en un solo nido.

4. Los huevos sin pedicelo se depositan sueltos o en series de dos a cuatro. Si al ponerlos no quedan arracimados, la hembra puede agruparlos activamente después. La nidada tiene un promedio de 23 huevos y no queda fija

a ningún objeto. Los huevos miden unos 5 mm de diámetro y se adhieren por la membrana externa. Se necesita atención persistente pero no constante de un adulto para el desarrollo ininterrumpido. Tanto machos como hembras toman parte en el cuidado de los huevos.

5. Después de un desarrollo calculado en cuatro o cinco meses, un joven completamente transformado rompe las dos membranas envolventes por medio de contorsiones violentas. Poco después de salir se retira a un lugar protegido. Durante los primeros dos años el crecimiento es relativamente rápido, probablemente de unos 5 mm por año; más tarde se reduce a un promedio bastante constante calculado en unos 3 mm por año. No se conoce ninguna diferencia sexual en la tasa de crecimiento.

6. Aunque la especie está activa durante la mayor parte de la noche, las horas de actividad son variables y sufren la influencia de la temperatura y, más frecuentemente, de la humedad. Los niveles máximos de actividad se observan a temperaturas de más de 6º C y a humedades relativas de más de 80%, y se reducen algo durante la precipitación misma. Probablemente entre el 10 y el 25% de la población cercana a la superficie está activa en una noche cualquiera.

7. La vagilidad es limitada en *B. subpalmata,* y cada individuo tiene un área definida de domicilio. No se halló ninguna diferencia estadística significativa entre los movimientos de machos, hembras y jóvenes ni en distancia ni en frecuencia. El área promedio de domicilio para todos estos grupos es de 44 m^2. No hay evidencia de que individuos desplazados regresen a su sitio anterior.

8. El apiñamiento parece ser una respuesta a condiciones desfavorables del ambiente, y no está relacionado con el comportamiento reproductivo. El evitar condiciones de extrema sequía o extrema humedad resulta en el hacinamiento en los sitios más favorables del habitat.

9. Las densidades de *B. subpalmata* en el Cerro de la Muerte llegan a proporciones notables y son determinadas localmente por factores independientes de la densidad, al tiempo que muestran correlación con la altitud. Las mayores densidades de población se encuentran cerca de la cumbre y en esta área pueden pasar de 9.000 animales por hectárea. Los cambios en la humedad tanto locales como estacionales influyen en la abundancia de animales en la superficie, y durante períodos secos se retiran a refugios subterráneos.

10. Los cálculos de la composición de las poblaciones por clases según la edad, que se confiesan especulativos, se basan en el tamaño de los individuos al salir del huevo y las tasas de crecimiento calculadas. La edad mayor alcanzada es de unos 18 años. Los machos aparentemente llegan a la madurez sexual en el sexto año, aunque no es sino hasta los doce años que la mayoría de las hembras han depositado huevos. Los machos no sólo maduran más pronto sino que llegan a la senilidad más temprano que las hembras. La proporción esperada de uno a uno entre los sexos se da en todas las estaciones y en todos los grupos por edad excepto el mayor, en el que las hembras exceden en mucho a los machos.

11. Las observaciones del número de nidadas y de hembras vacías se

usan para determinar una capacidad potencial reproductiva parcial anual calculada en 58%.

12. Los cómputos de supervivencia y mortalidad, según diversos métodos matemáticos, son tan variables que hacen dudar seriamente la validez de la aplicación de muchos de estos métodos a poblaciones de salamandras. La fluctuación de la densidad de las poblaciones, el uso muy extenso del habitat y los bajos niveles de actividad contribuyen a crear problemas en el uso de registros de recaptura. La ausencia constante de individuos inmaduros de las muestras presenta problemas casi invencibles en el uso de datos de captura única.

13. Los mejores cálculos disponibles de supervivencia anual son de entre 0,29 y 0,65, decreciendo con la edad. No ha sido posible construir tablas de vida o curvas de supervivencia. La capacidad reproductiva potencial elevada y los factores de mortalidad en adultos sugieren que debe haber una elevada mortalidad juvenil y de las nidadas. Además, la falta de una fidelidad fuerte en el cuido de las nidadas por los adultos y la falta de comportamiento de regreso en *B. subpalmata* suman indicios de una alta mortalidad de los huevos.

14. Las necesidades de humedad de esta especie son semejantes a las de varias pletodóntidas extratropicales. La humedad total del cuerpo da un promedio de cerca de 80% del peso del cuerpo. No se nota comportamiento de tensión en animales que pierden hasta el 32,3% del peso inicial, aunque ninguno sobrevivió a una pérdida de más del 41,2%. La tasa de pérdida de agua dio un promedio de 2,5% por hora, pero es algo mayor en animales pequeños. En todos los individuos se reduce la pérdida de agua por un comportamiento de apiñamiento. La rehidratación se realiza hasta seis veces más rápidamente que la deshidratación a una misma temperatura. La velocidad de reabsorción de agua en ambiente saturado es menor que la de un individuo sumergido en líquido; pero este último ambiente no ofrece ninguna ventaja ecológica, o muy poca a lo sumo.

15. Sumergidas en el agua, las salamandras pierden la capacidad de enderezarse después de períodos que varían desde 3,50 a 7,75 horas (promedio 5,35). El cese de circulación capilar se observó después de 6,75 a 17,50 horas (promedio 10,14). La diferencia promedio entre estos períodos fue de 3,30 horas.

16. La humedad del suelo ejerce gran influencia sobre la ocupación de la superficie de las áreas habitadas. A menos de 30%, las salamandras están virtualmente ausentes: el nivel óptimo está entre 55 y 75%.

17. Las salamandras adultas pueden sobrevivir a exposiciones prolongadas a temperaturas entre 4 y 24° C. A temperaturas de congelación (-4,0° C) la muerte sobreviene generalmente en menos de dos horas. Las temperaturas de 27° C son letales después de 72 horas, mientras que a 37° C se produce casi inmediatamente un shock térmico mortal.

18. Los límites térmicos ecológicos están probablemente a un nivel fijo de unos 16° C, más alto de lo cual no se ponen huevos. El máximum crítico térmico (CTM) de aproximadamente 37° C se considera aquí como un máximum fisiológico más que ecológico, y no el límite de tolerancia en la etapa más susceptible del ciclo vital.

19. La temperatura del cuerpo varía muy poco de la del microhabitat. El ámbito de variación de temperaturas toleradas voluntariamente es de 2,8 a 23,8° C (una diferencia de 21° C), lo cual es más que lo relatado de ninguna otra especie pletodóntida.

20. Los pletodóntidos de la zona templada ocupan una variedad mayor de habitats que los de los trópicos. No se conoce ninguna especie tropical acuática. Probablemente ha habido poca ventaja selectiva en el regreso al agua después de la evolución del desarrollo directo. Ninguna especie de la familia sobrepasa a *B. subpalmata* en utilización del habitat.

21. Los pletodóntidos tanto tropicales como extratropicales faltan generalmente en zonas donde la precipitación anual es menos que la evapotranspiración potencial, excepto donde las condiciones locales modulan estos factores. Los límites mínimos de temperatura están probablemente muy cerca del nivel de 6° C de biotemperatura. La distribución en altitud de diversas especies tropicales indica adaptaciones a distintos niveles térmicos.

22. En los géneros de pletodóntidos se observa tres tipos de patrón reproductivo. *Desmognathus* comprende especies de todos estos patrones. Es muy probable que todas las especies tropicales tengan desarrollo directo como *B. subpalmata.*

23. Los pletodóntidos extratropicales tienen períodos de cría notablemente escalonados, tanto como poblaciones como en cuanto especies. La reproducción acíclica en *B. subpalmata* maximiza el uso de los sitios disponibles para nido y permite eludir a nivel de población los cambios físicos desfavorables de corta duración en el ambiente.

24. La producción de lóbulos testiculares es aparentemente una manifestación de los límites impuestos por las capacidades metabólicas del tejido germinativo primordial, y no tiene correlación con la periodicidad del ambiente. La oviposición bienal está limitada por condiciones intrínsecas similares.

25. Se sugiere que, de las funciones probablemente múltiples del comportamiento de cría, la manipulación de los huevos por el adulto satisface un requisito cinético vital que impide el desarrollo de adherencias en el desarrollo, siendo en parte análogo a una función amniótica.

ADDENDUM

Since June 7, 1965, when this report was submitted for publication, several pertinent articles have appeared. It is not possible to incorporate these works by revision or extensive supplementation. Of particular note, however, is the report by VALDIVIESO and TAMSITT (*Herpetologica* 21: 228-236) of an acyclic reproductive pattern in the Colombian salamander, *Bolitoglossa adspersa.* They also observed significant size differences between males and females at the attainment of maturity. Gravid females and mature males were taken during nine nonconsecutive months and eggs were found four months of the year. A sample of males showed polymodal size relationships to the number of testicular lobes, which they interpreted as representing consecutive seasons in a continuously breeding population.

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Fig. 1. Costa Rica, Central América, showing the location of the study area (represented by hatching) in the Cordillera de Talamanca.

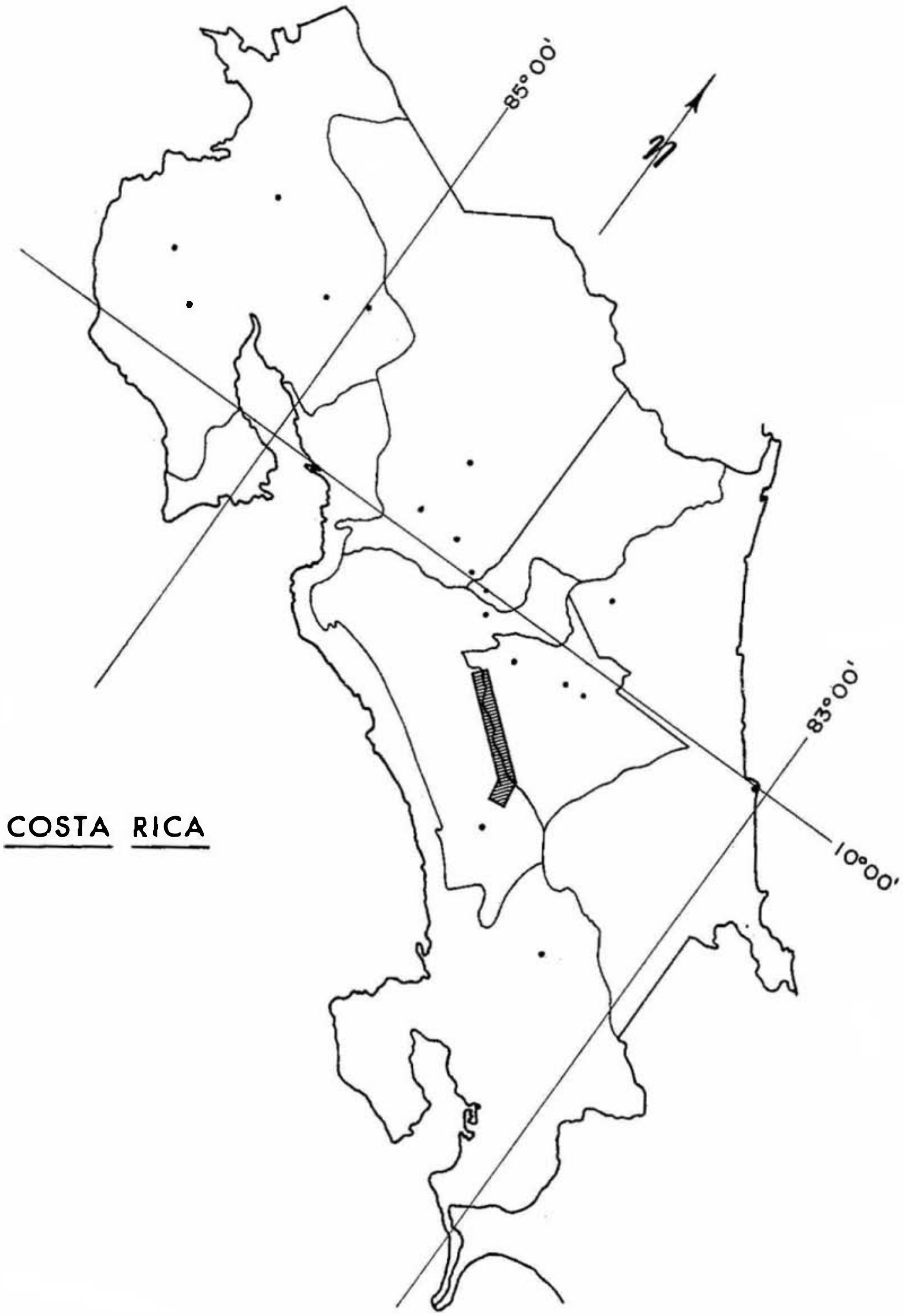

85° 00'
N
83° 00'
10° 00'
COSTA RICA

Fig. 2. Detail of the study area transect formed by the Inter-American Highway through the Cerro de la Muerte, Cordillera de Talamanca of Costa Rica. Localities and place names were taken from aerial photographs and topographic sheets issued by the Inter-American Geodetic Survey in cooperation with the Instituto Geográfico de Costa Rica. Elevations designated by "x" are from survey points, others are aneroid readings. Elevations are in meters. WS = Weather Station, Q = Quadrat Site, Pop. N = Location and Number of Marked Population, BM = Bench Mark.

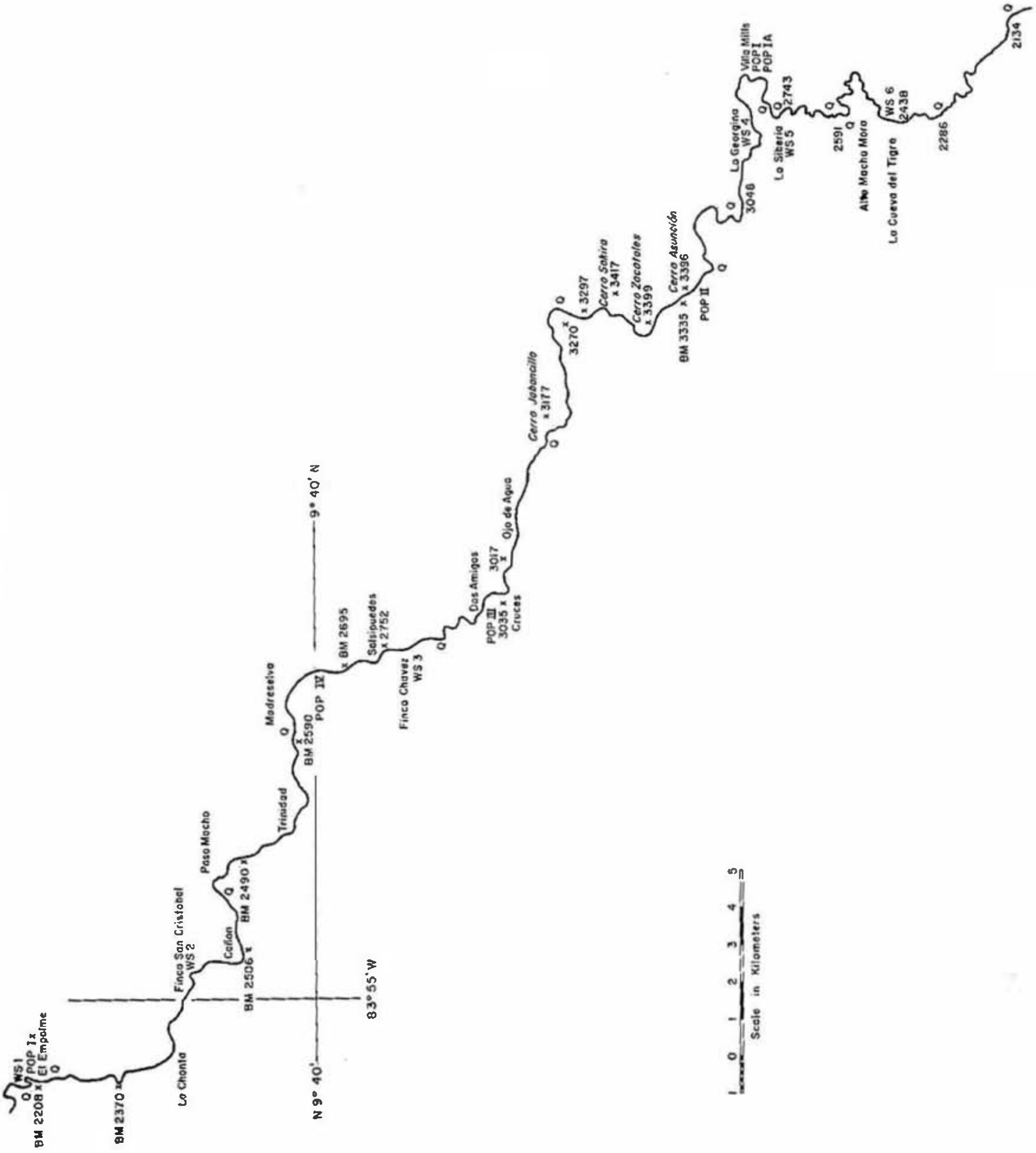
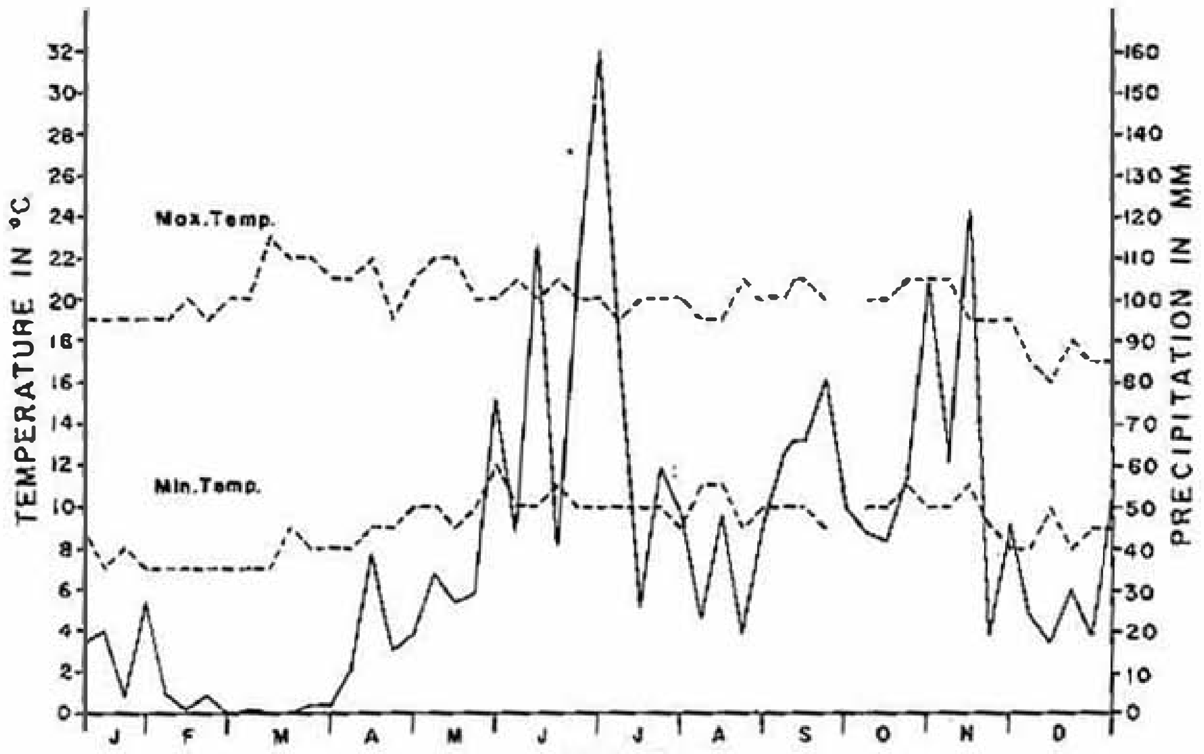

BM 2208 x
WS 1
POP I x
El Empalme
BM 2370
La Chonta
Finca San Cristobal
WS 2
BM 2506 x
Cañon
BM 2490 x
Paso Macho
Trinidad
BM 2590
POP IV
Madreselva
x BM 2695
Salsipuedes
x 2752
Finca Chavez
WS 3
POP III
3035 x
Cruces
Dos Amigos
3017
Ojo de Agua
Cerro Jaboncillo
x 3177
3270
x 3297
Cerro Sakira
x 3417
Cerro Zacatales
x 3399
BM 3335 x
POP II
Cerro Asunción
x 3396
3046
La Georgina
WS 4
Villa Mills
POP I
POP IA
La Siberia
WS 5
2743
2591
Alto Macho Mora
WS 6
2438
La Cueva del Tigre
2286
2134
N 9° 40'
9° 40' N
83° 55' W
0 1 2 3 4 5
Scale in Kilometers

Fig. 3. Climatic regimen at El Empalme (2,134 m) showing precipitation, maximum and minimum temperatures based upon weekly readings for the year, September 15, 1961, to September 15, 1962.

Fig. 4. Climatic regimen at La Georgina (3,048 m) showing precipitation, maximum and minimum temperatures based upon weekly readings for the year, September 15, 1961, to September 15, 1962.

Fig. 5. Correlation of biotemperatures and elevations on the Cerro de la Muerte. Open circles represent records from weather stations. Estimated value for the summit of the study area is extrapolated at the intersection of lines placed by inspection.


Max.Temp.
Min.Temp.
TEMPERATURE IN °C
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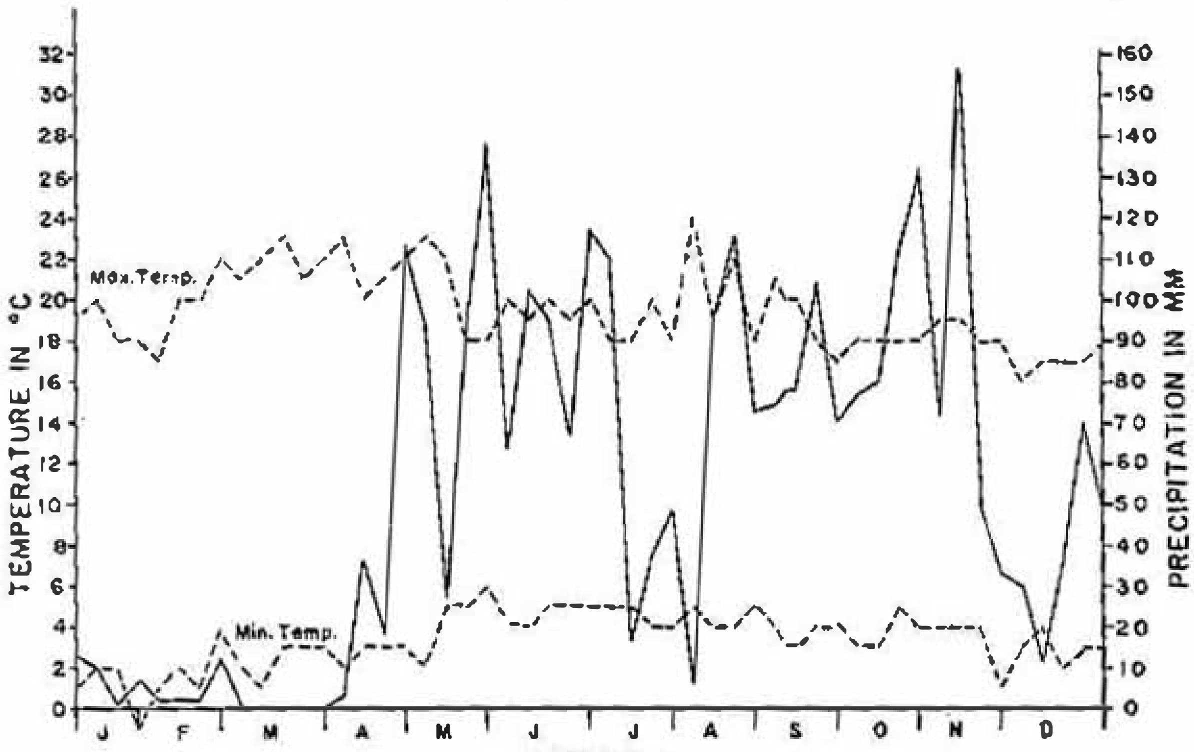
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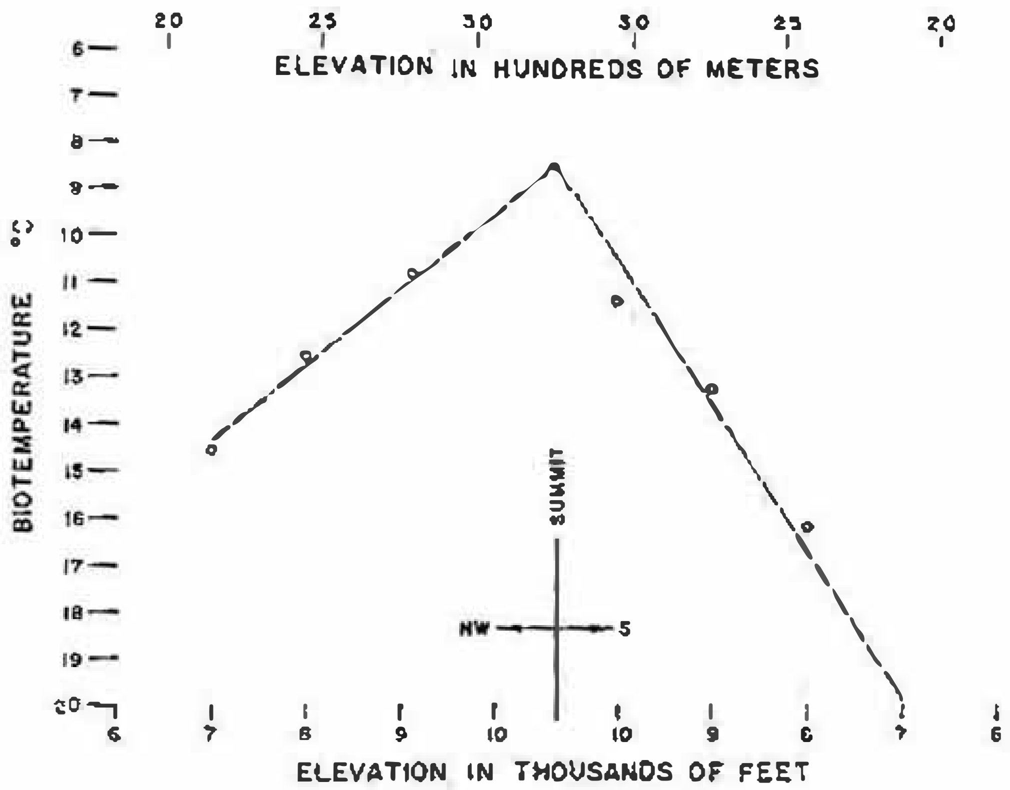
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ELEVATION IN HUNDREDS OF METERS
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ELEVATION IN THOUSANDS OF FEET

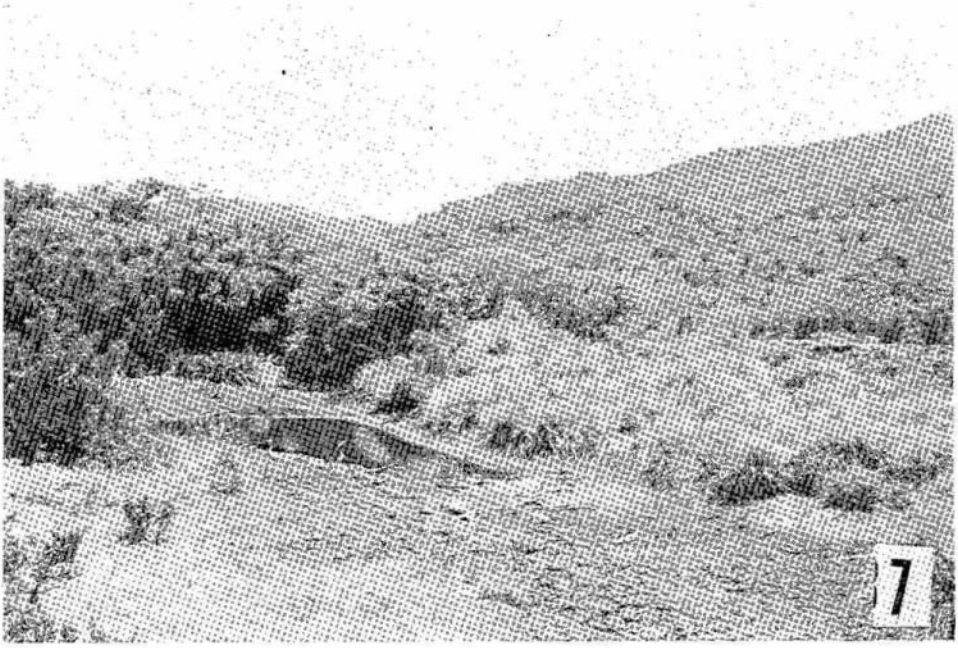
5

Fig. 6. The Tropical Lower Montane Wet Forest near Trinidad (2,500 meters). Principal tree species occurring at this locale include *Quercus copeyensis, Persea Schiedeana, Magnolia poasana, Cornus disciflora* and *Clusia alata.*

6

Fig. 7. The páramo or subalpine wet woodland of Costa Rica near the summit of the Cerro de la Muerte. Actually a poorly defined disclimax community in this region, it includes many of the Tropical Montane Rain Forest components. Predominant plants in the photograph include *Chusquea subtessellata, Pernettya coriacea, Escallonia poasana* and *Buddleia alpina.*

Fig. 8. General aspect of an edaphically limited plant community at 2,800 m on the Cerro. Predominant species on such poorly developed soils include the tree fern *Lomaria loxensis,* a terrestrial bromeliad *(Puya dasylirioides)* and *Hypericum strictum.*

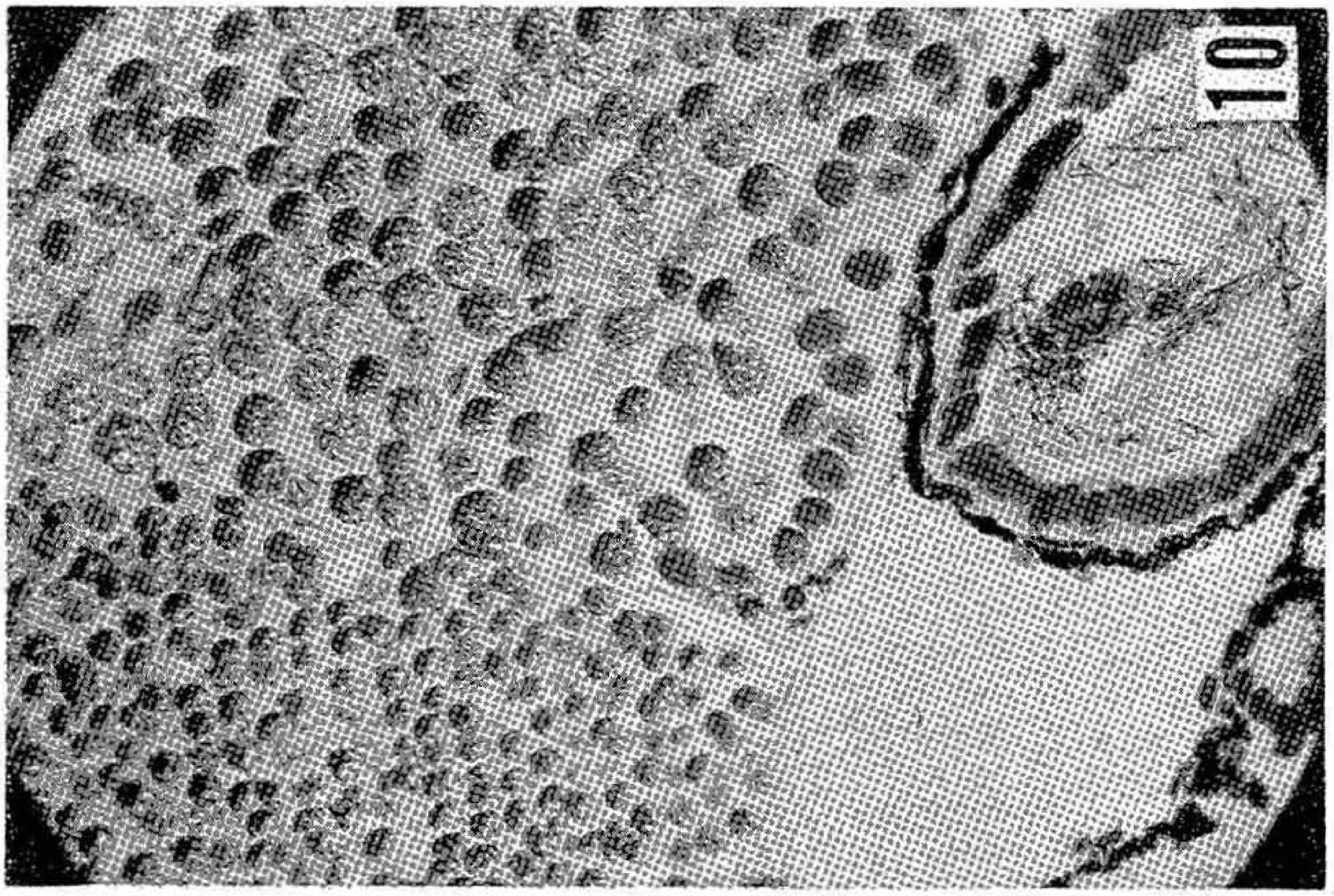


7

8

Fig. 9. Photomicrograph of single-lobed testis of *B. subpalmata* viewed under 100 diameters and enlarged. In the lower right of the lobe can be seen enlarged spermatocytes I. Lobules in the upper left contain the conspicuously smaller spermatocytes II. Visible in the extreme upper left is one lobule containing spermatids.

Fig. 10. Photomicrograph of the mid-region of a testis, viewed under 250 diameters and enlarged, showing detail of lobule formation and a uniform content of spermatocytes I or smaller spermatocytes II. In the lower margin the dark lines included in the lumen of the vas deferens are spermatozoa.



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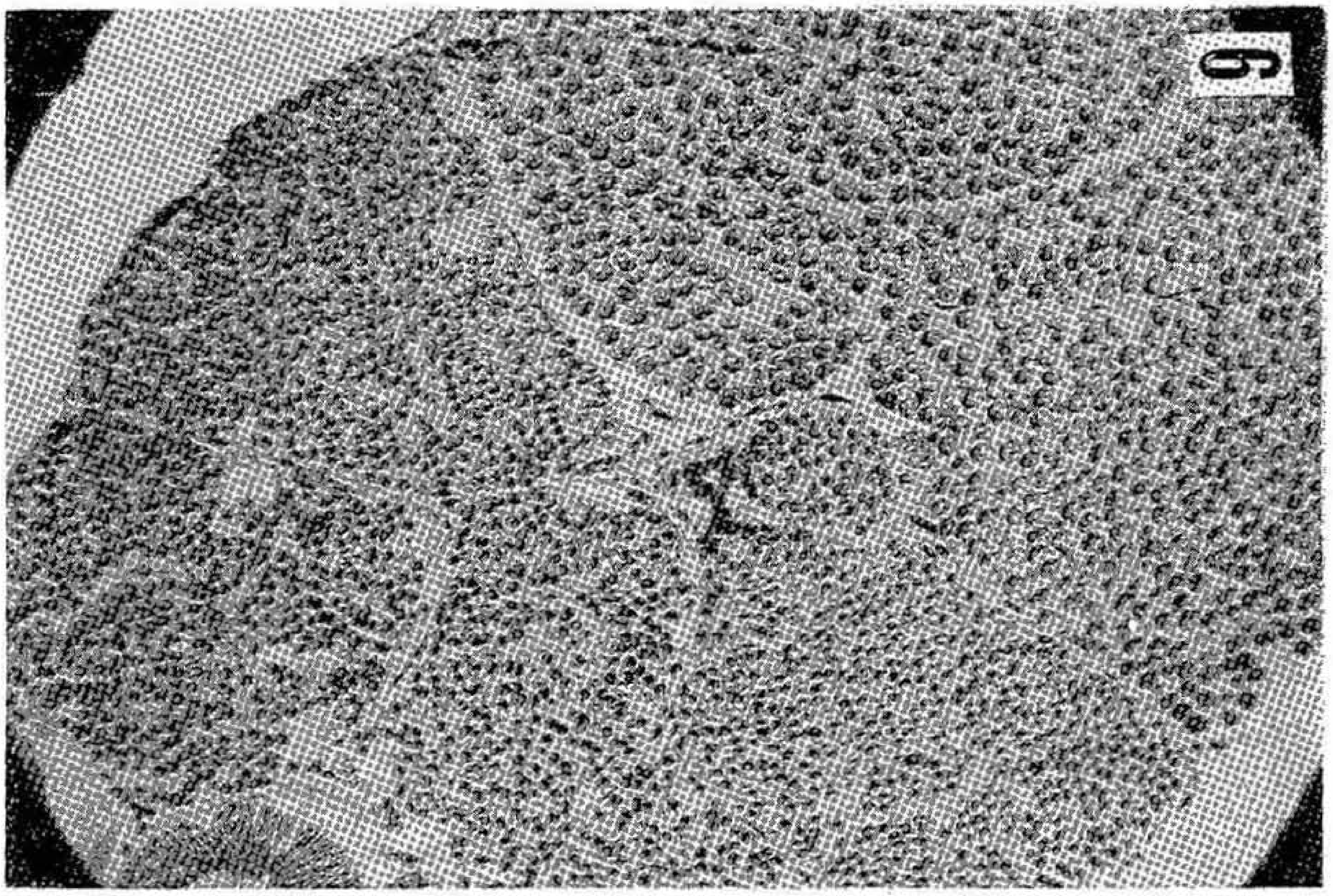


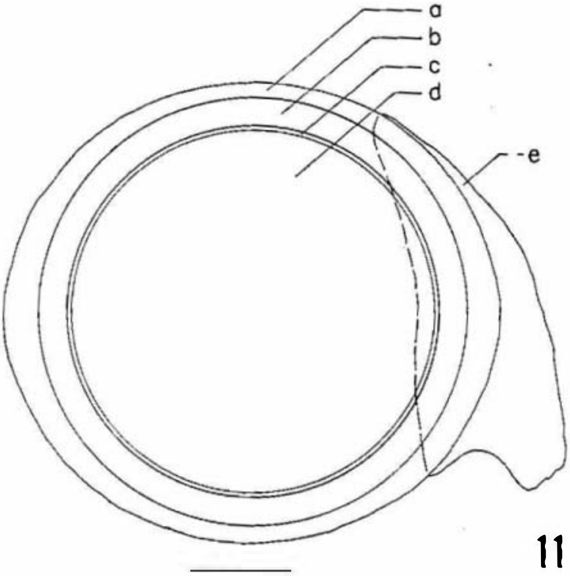
9

Fig. 11. Drawing of a newly deposited egg of *B. subpalmata.* Abbreviations: a = outer gelatinous envelope; b = inner gelatinous layer; c = extraovular space;. d = yolk; e = torn remnant of adhesive surface of outer membrane. Line represents scale of one mm.

Fig. 12. Neural groove stage of an early embryo of *B. subpalmata.* The enveloping gelatinous membranes are omitted.

Fig. 13 Optic vesicle stage, dorsal view. Note that posterior part of embryo is capable of flexion. Outer-most circle represents inner margin of gelatinous envelope.

Fig. 14. Lateral view of same embryo shown in Figure 13.



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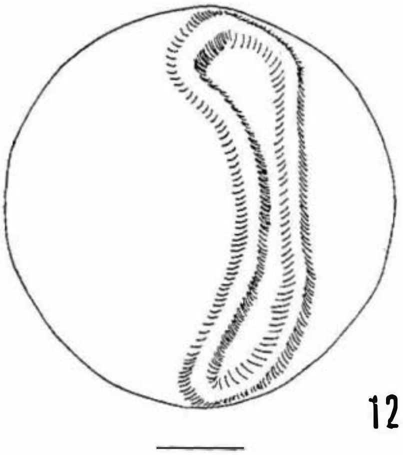

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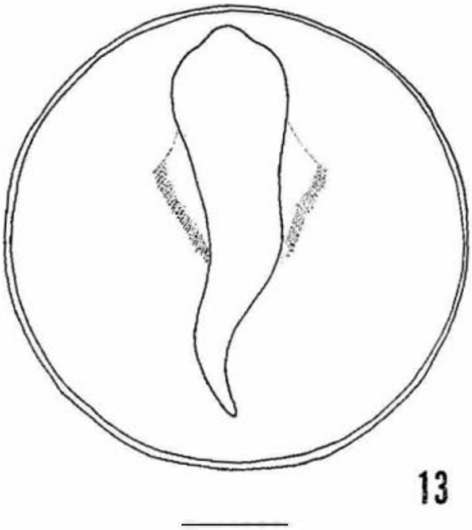

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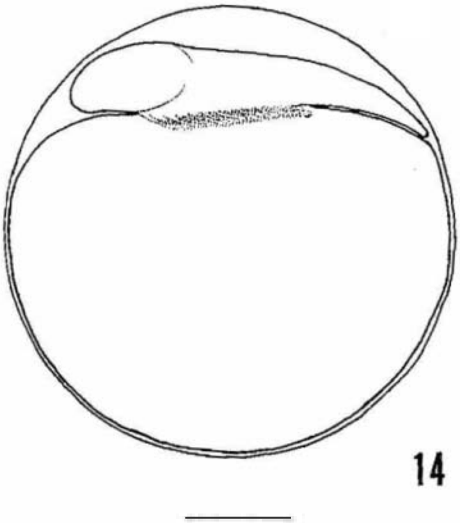


14

Fig. 15. Early limb bud formation in *B. subpalmata*, dorsal view. Gills are already tripartite in the unpigmented embryo.

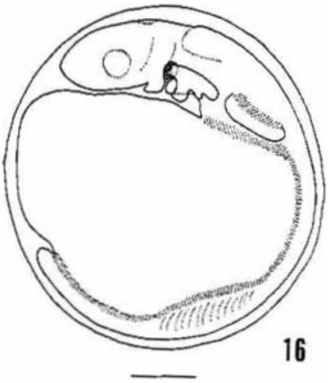
Fig. 16. Lateral view of same embryo shown in Figure 15.

Fig. 17. Early pigmentation stage. Sparse stellate melanophores occur diffusely over the body except for the vertebral region and the unarticulated limbs.

Fig. 18. Late embryo before fusion of costal segments. Pigmentation, although well developed, is not shown. Note the appearance of toes and reduction of gills.

Fig. 19. Embryo immediately before hatching. Pigmentation is not shown. Note further reduction of allantoic gills to thin filaments.

15



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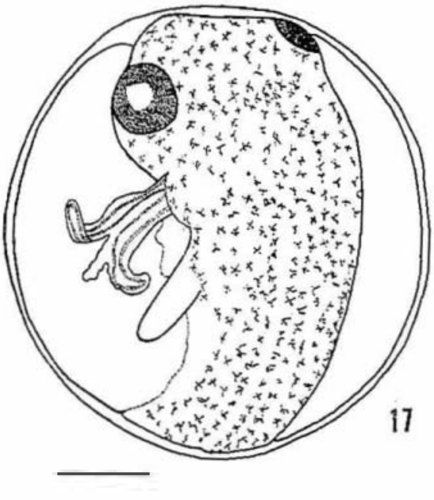

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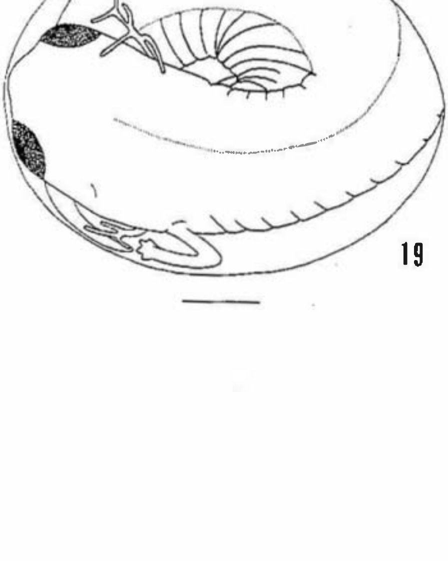


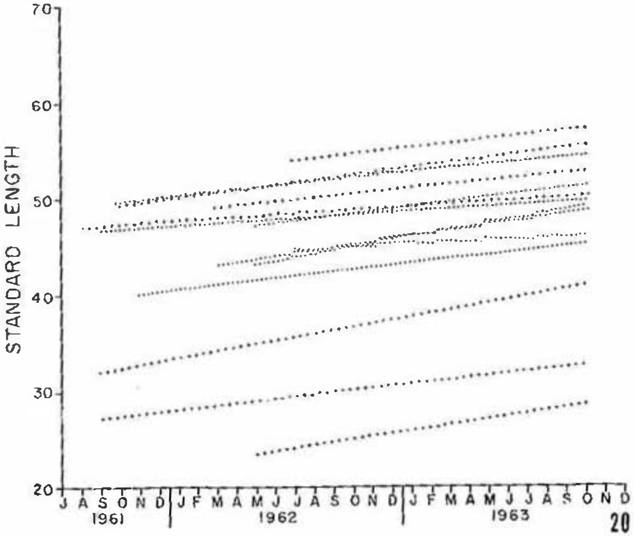
19

Fig. 20. Individual growth patterns of fourteen *B. subpalmata* recaptured in October, 1963. Records obtained between first and last captures are not included. Males are shown by dotted lines; females by crossed line.

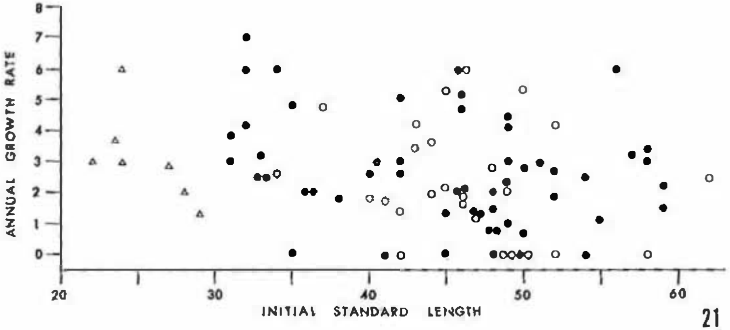
Fig. 21. Computed annual growth rates of 87 individuals including males, females and juveniles, plotted against initial standard length. Triangles represent juveniles; dots the females; and circles the males.

Fig. 22. Average annual growth rates for the observed size classes of *B. subpalmata*. Each circle represents the average of the above zero values included in Figure 21.

Fig. 23. Size-age classes and growth curve of *B. subpalmata*.


STANDARD LENGTH
70
60
50
40
30
20
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1961
1962
1963

20


ANNUAL GROWTH RATE
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7
6
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4
3
2
1
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20
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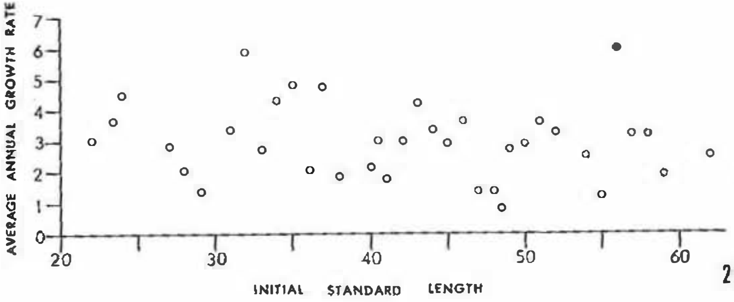
40
50
60
INITIAL STANDARD LENGTH

21


AVERAGE ANNUAL GROWTH RATE
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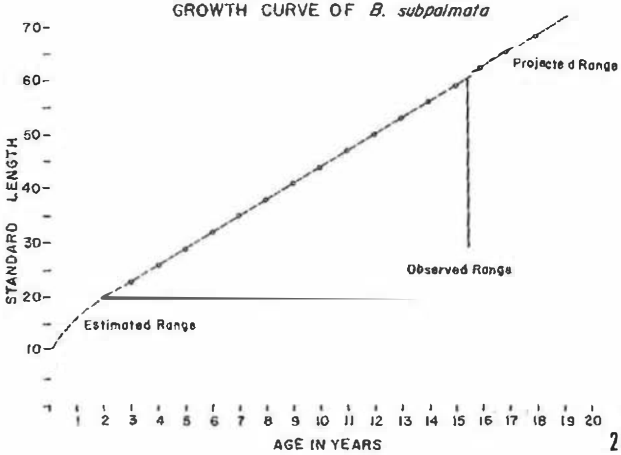
50
60
INITIAL STANDARD LENGTH

22

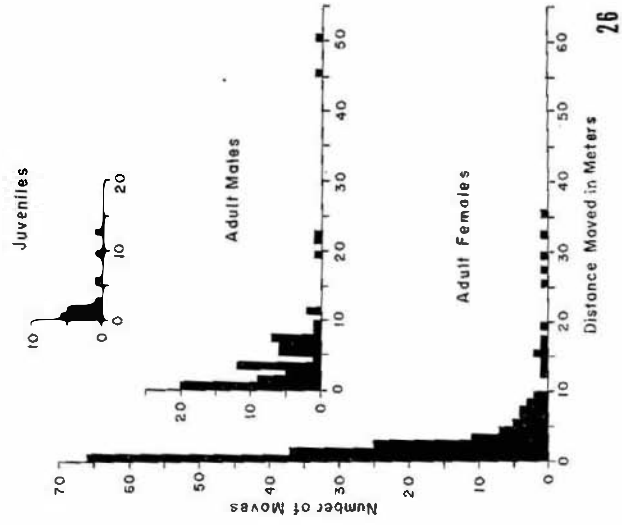

GROWTH CURVE OF B. subpalmata
STANDARD LENGTH
70
60
50
40
30
20
10
Projected Range
Observed Range
Estimated Range
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
AGE IN YEARS

23

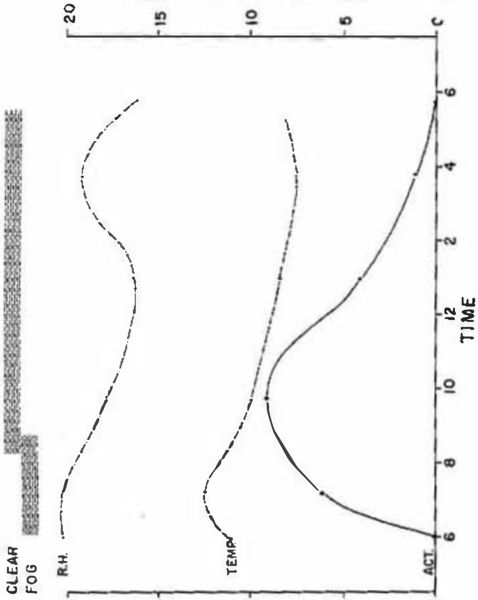
Fig. 24. A unimodal nocturnal activity cycle of *B. subpalmata* observed at Population III on September 18-19, 1961. Observations are expressed in units of percentage of total activity during that period. Soil-air interface temperatures, relative humidity and weather conditions are given for each two hour observation interval. Black dot represents time of record.

Fig. 25. A bimodal nocturnal activity cycle of *B. subpalmata* observed at Population II on May 12-13, 1962. The manner of presentation is the same as for Figure 24.

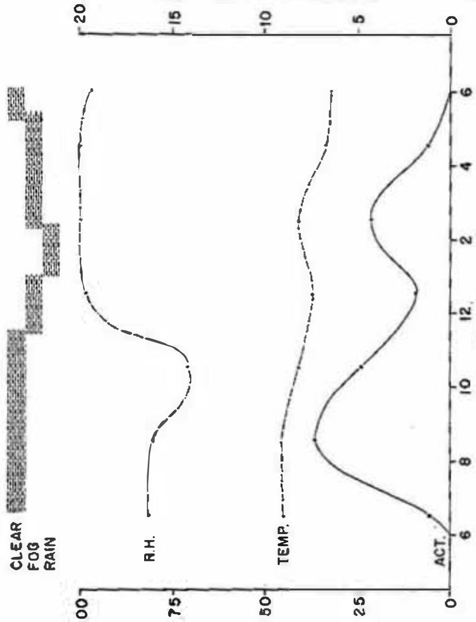
Fig. 26. Frequencies of movements of males, females and juveniles at distance intervals of one meter.


Juveniles
10
0
0
10
20
Adult Males
20
10
0
0
10
20
30
40
50
Adult Females
Number of Moves
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
Distance Moved in Meters

26


CLEAR
FOG
R.H.
TEMP.
ACT.
% ACTIVITY — RELATIVE HUMIDITY
100
75
50
25
0
TIME
6
8
10
12
2
4
6
TEMPERATURE °C
20
15
10
5
0

24


CLEAR
FOG
RAIN
R.H.
TEMP.
ACT.
% ACTIVITY — RELATIVE HUMIDITY
100
75
50
25
0
TIME
6
8
10
12
2
4
6
TEMPERATURE °C
20
15
10
5
0

25

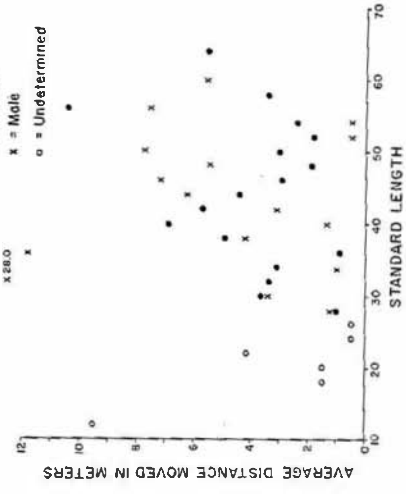
Fig. 27. Average distances moved in relation to standard length for males, females and juveniles.

Fig. 28. Average number of moves in relation to size for males, females and juveniles. See Figure 27 for explanation of symbols.

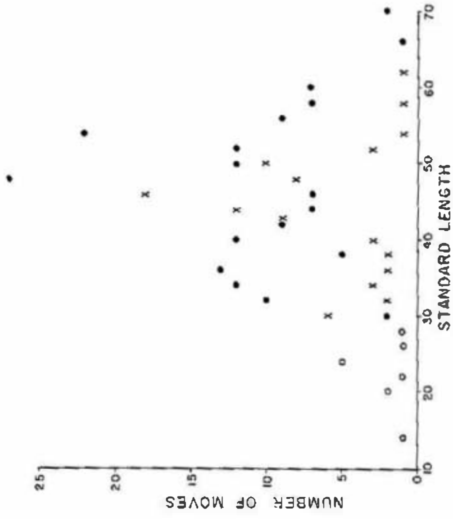
Fig. 29. Relative densities of *B. subpalmata* plotted against biotemperatures of different quadrat sites on the Cerro de la Muerte.

Fig. 30. Computed ecological densities of three marked populations on the Cerro, plotted as number of animals per square meter for each monthly observation. Black circles represent computed densities on basis of recapture data. Open circles denote computations in absence of any recaptures (see text). Roman numerals are field designations of the populations. "P" equals precensus period.

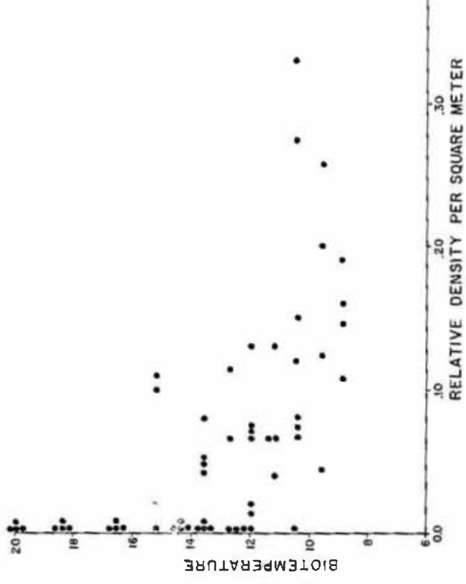
DISTANCE OF MOVES IN RELATION TO SIZE



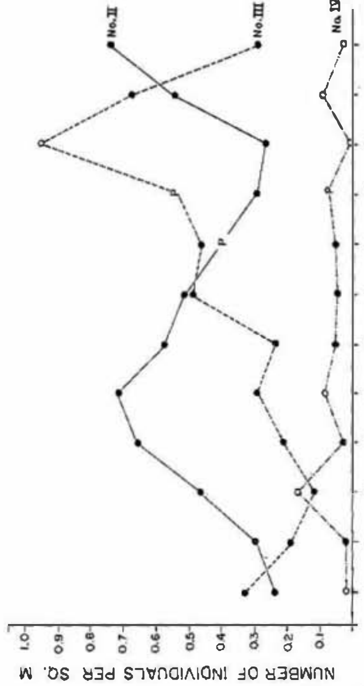
27



28



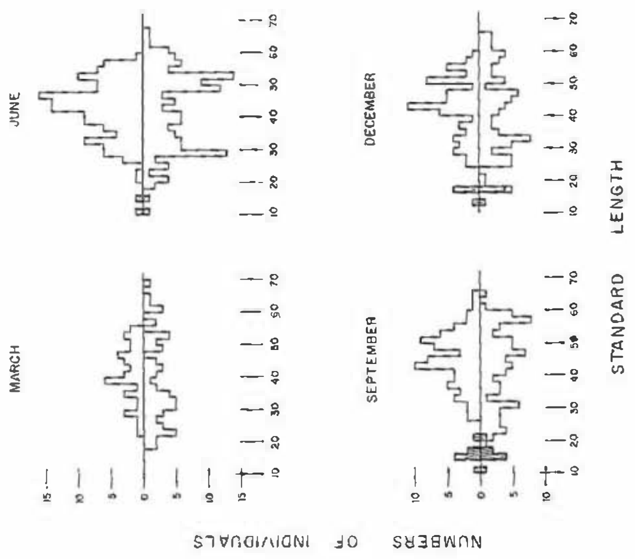
29



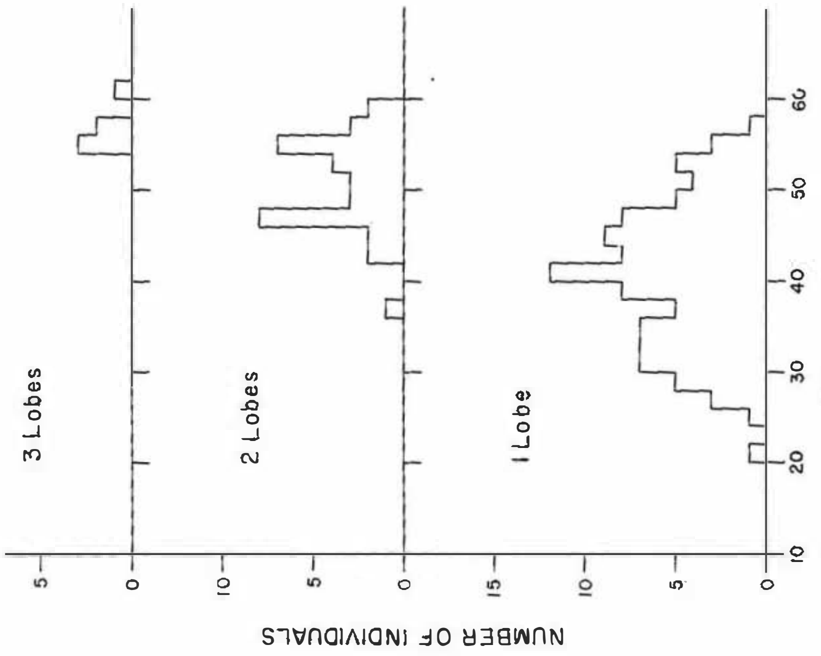
30

Fig. 31. Size and sexual composition of total samples from quarterly quadrats of *B. subpalmata* taken on the Cerro de la Muerte, plotted at 2.0 mm intervals. Males are represented above the zero abscissa, females below. Undetermined specimens are indicated by vertical bars and are included both above and below the zero abscissa.

Fig. 32. Size classes of male *B. subpalmata* plotted at [illegible] mm size intervals showing frequency of occurrence of one, two or three testicular lobes.


MARCH
JUNE
SEPTEMBER
DECEMBER
NUMBERS OF INDIVIDUALS
STANDARD LENGTH
15
10
5
0
5
10
15
10
20
30
40
50
60
70

31

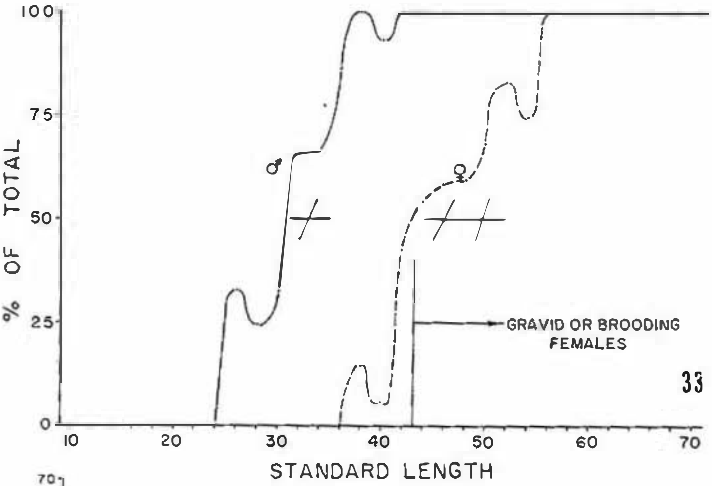

3 Lobes
2 Lobes
1 Lobe
NUMBER OF INDIVIDUALS
STANDARD LENGTH
5
0
10
5
0
15
10
5
0
10
20
30
40
50
60

32

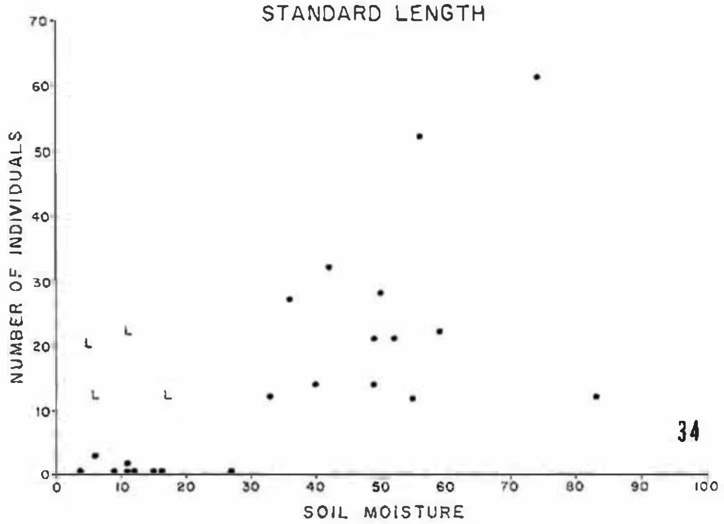
Fig. 33. Sexual maturity of *B. subpalmata* populations expressed as percentage of total observations. Intersection of slanted line with 50% abscissa indicates size class at class at which 50% of that sex has reached maturity.

Fig. 34. Relative densities of quadrat samples compared to soil moistrue. The actual number of collected specimens is plotted against percentage of dry weight of the soil sample. "L" denotes that only localized aggregations were found.

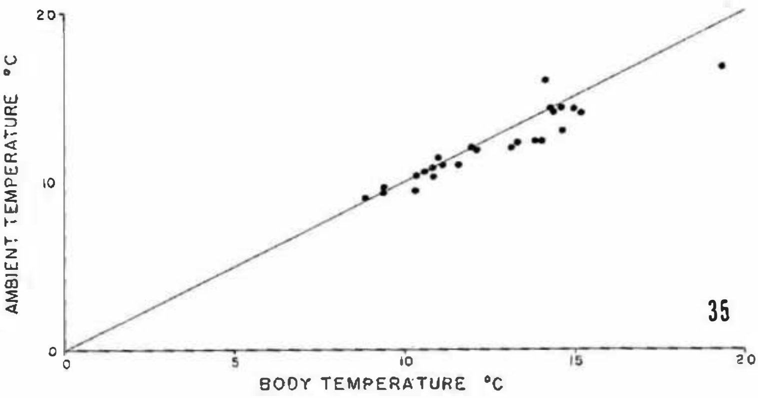
Fig. 35. Cloacal temperatures of *B. subpalmata* plotted against soil-air interface temperatures. The inclined line represents the points at which body and ambient temperatures are equal.


% OF TOTAL
100
75
50
25
0
♂
♀
GRAVID OR BROODING FEMALES
10
20
30
40
50
60
70
STANDARD LENGTH

33

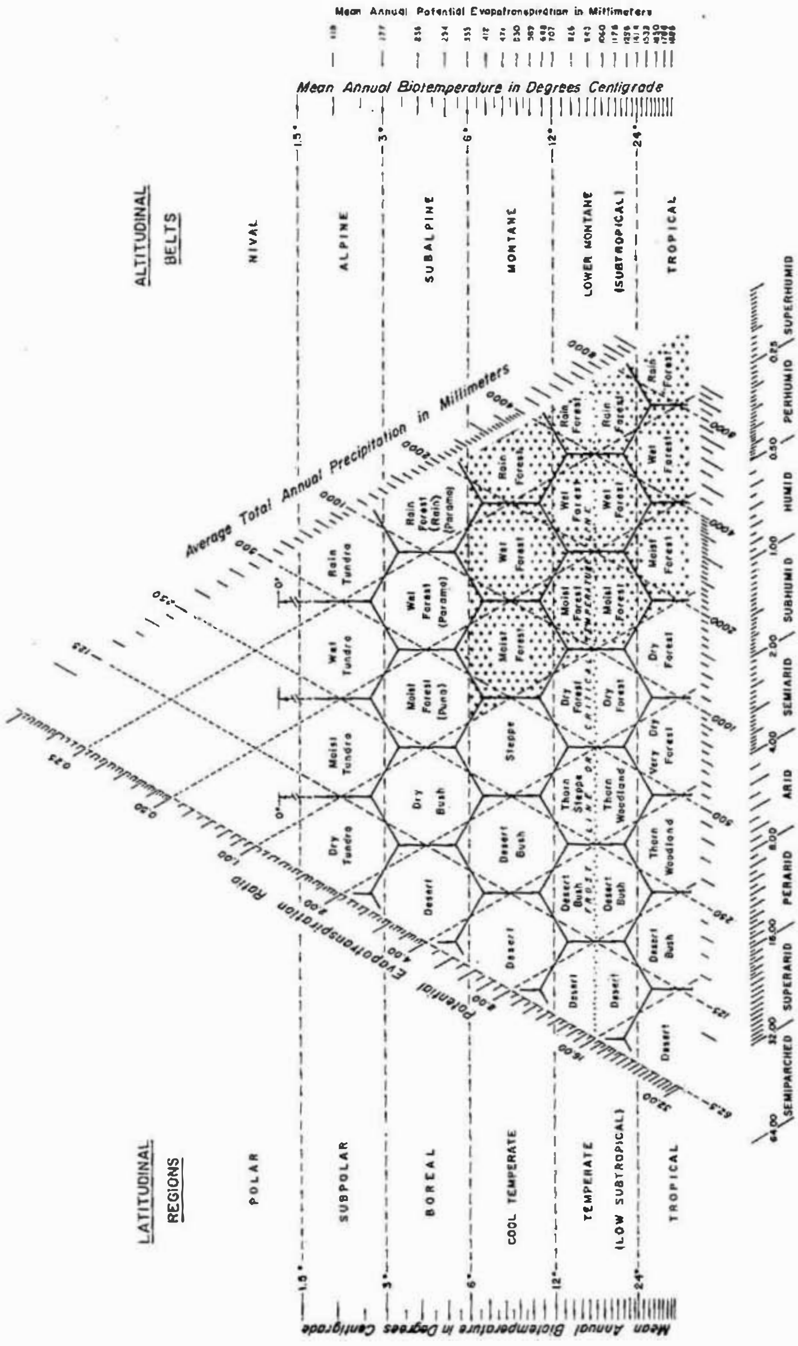

NUMBER OF INDIVIDUALS
70
60
50
40
30
20
10
0
L
0
10
20
30
40
50
60
70
80
90
100
SOIL MOISTURE

34


AMBIENT TEMPERATURE °C
20
10
0
0
5
10
15
20
BODY TEMPERATURE °C

35

Fig. 36. System of classification of world plant formations on a climatic basis by L. R. Holdridge (39, 42). The ecological regions and belts, as well as the vegetation formations occupied by plethodontid salamanders are indicated by stippling.


LATITUDINAL REGIONS
POLAR
SUBPOLAR
BOREAL
COOL TEMPERATE
TEMPERATE
(LOW SUBTROPICAL)
TROPICAL
ALTITUDINAL BELTS
NIVAL
ALPINE
SUBALPINE
MONTANE
LOWER MONTANE
(SUBTROPICAL)
TROPICAL
Mean Annual Biotemperature in Degrees Centigrade
1.5°
3°
6°
12°
24°
Mean Annual Potential Evapotranspiration in Millimeters
Average Total Annual Precipitation in Millimeters
Potential Evapotranspiration Ratio
HUMIDITY PROVINCES
SEMIPARCHED
SUPERARID
PERARID
ARID
SEMIARID
SUBHUMID
HUMID
PERHUMID
SUPERHUMID
Dry Tundra
Moist Tundra
Wet Tundra
Rain Tundra
Desert
Dry Bush
Moist Forest (Puna)
Wet Forest (Paramo)
Rain Forest (Rain) (Paramo)
Desert Bush
Steppe
Moist Forest
Wet Forest
Rain Forest
Desert Bush
Thorn Steppe
Dry Forest
Moist Forest
Wet Forest
Rain Forest
Thorn Woodland
Dry Forest
Very Dry Forest
Thorn Woodland
Desert Bush
Desert
FROST LINE OR CRITICAL TEMPERATURE LINE