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A Herpetofaunal Study of an Ecological Transect Through the Cordillera de Tilarán, Costa Rica

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Herpetofaunal distribution patterns were examined along a 25 km transect in northern Costa Rica to determine the relationship of faunal occurrence to vegetation zones. The herpetofaunal sample comprised 1929 specimens representing 136 species. Large samples were available for five localities. Coefficient of difference (C.D.) values of species in common indicate that these five samples represent four distinct faunal assemblages. The total distributional data were also transcribed onto a chart, and the areas of greatest faunal change were determined. This analysis corroborated the presence of four herpetofaunal assemblages, and indicated 13 major patterns of distribution along the transect.

The distribution of the herpetofaunal assemblages and the six vegetation zones of the transect were found to be closely correlated. One herpetofaunal assemblage is distributed in the Tropical Dry Forest and Subtropical Moist Forest zones. A second assemblage is found in the Tropical Moist Forest and the lower Subtropical Wet Forest zones. A third is found in the upper portion of the Subtropical Wet Forest and Subtropical Rain Forest zones. The fourth assemblage is associated with Tropical Wet Forest vegetation.

C.D. values for two samples from comparable altitudes on opposite sides of the Cordillera de Tilarán indicate that they represent different herpetofaunal assemblages, and that herpetofaunal zonation is not strictly altitudinal. Two herpetofaunal samples from the same vegetation zone but from different sides of the continental divide were compared and found to represent the same herpetofaunal assemblage. Thus Atlantic-Pacific slope differences are not major factors affecting herpetofaunal distribution patterns in the transect area.

Observations in the transect area suggest that herpetofaunal distributions correlate with specific microhabitats associated with particular vegetation zones, or are limited by climatic factors.

The herpetofaunal zones of this transect are narrower and more sharply defined than those of Grinnell and Storer's (1924) extratropical Yosemite transect. The life zone concept appears valid in analyzing tropical herpetofaunas.

Introduction

THE original discussion of the life zone concept (Merriam, 1890) was based on distributional data for the vegetation and several animal groups of the San Francisco Peak region in Arizona. The environmental determinants that Merriam emphasized in delineating the life zones have not proved to be applicable universally (for a review, see Daubenmire, 1938), but the basic theory of the life zone as a latitudinal or altitudinal zone regulated by climate and characterized by a distinctive association of vegetation and fauna has become recognized as an important ecological concept. Although Carriker

[1] Supplemental (appendix) material to this article has been deposited as Document No. 9165 with the ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington, D. C. 20540. A copy may be secured by citing the document number and remitting $1.25 for photoprints, or $1.25 for 35 mm microfilm. Advance payment is required. Make checks or money orders payable to: Chief, Photoduplication Service, Library of Congress.

(1910) and Griscom (1932) have attempted to extend Merriam's concept to the tropical latitudinal regions, the majority of studies on biotic zonation are based on extratropical situations (e.g., Dice, 1943).

Zonation studies in tropical areas have resulted in different interpretations of the relationship between faunal distribution and vegetational zones. Ornithologists working in the tropics long have noted the apparent dependence of the avifauna on vegetational types (Carriker, 1910; Chapman, 1917; Slud, 1960, 1964). Biologists working with the distributional patterns of amphibians and reptiles in tropical areas have reached conflicting conclusions regarding the validity of a fauna to vegetation zone correlation. Studies that have shown general concordance between herpetofaunal distribution and vegetation zones include: Brown and Alcala (1961) for the Philippine Islands; Martin (1958) for the Gómez Farías Region, Tamaulipas, México; and Wake (1964) for Costa Rica.

Two workers have expressed doubt as to the validity of correlating faunal distribution with vegetation zones in the Central American tropics, Duellman (1960, 1963) and Stuart (1950, 1954, 1955). Stuart (1955: 8) in questioning this relationship stated: "It may be noted in passing that any effort to arrange the anoles of Guatemala geographically on the basis of the 'life zone' approach can lead only to a false picture of its [sic] distribution."

In his statement, Stuart touched upon two concepts; life zone and biotic area. The meanings of these terms have been confused in recent years. In the present analysis a life zone is defined as an ecological altitudinal or latitudinal zone, characterized by specific climatic parameters and secondarily by vegetation. Equivalent life zones may be represented in widely separated geographic regions (tropical Africa and South America, for example). A biotic area, in contrast, is a geographic region characterized by a unique composition of flora and fauna. A biotic area may encompass several life zones. The concept of a life zone emphasizes the interaction of ecologic factors as they regulate current distribution patterns and minimizes the importance of historical factors. The interactions of the historic factors are the significant elements in the biotic area concept, since they regulate the composition and dispersal of the biota.

Two climatic features distinguish tropical from extratropical regions: 1) climatic patterns are more uniform on a daily and yearly basis in the tropics than in the extratropics, 2) certain climatic factors such as rainfall and temperature play different ecologic roles in the two regions (Vial, 1965). Two other major ecologic differences are the comparative richness of species and the historically long climatic stability of the tropics as opposed to the extratropical areas (Richards, 1963).

The purpose of this paper is to answer the question, "Do ecologic life zones under tropical conditions support distinctive herpetofaunal assemblages or is the fauna distributed continuously or in patterns not corresponding to altitude, climate, and vegetation?"

Previous studies have not conclusively demonstrated a relationship between faunal distribution and life zones in the tropics for the following reasons: 1) Most areas studied were too large, involving large geographic areas; study of a geographic entity necessarily involves consideration of historical factors, and de-emphasizes contemporary ecological influences; 2) the size of the study area was appropriate, but the ecologic variety was minimal, precluding analysis of the relations between faunal assemblages and ecologic zones.

Northern Costa Rica contains an almost straight line road transect through the northern extent of the Cordillera de Tilarán. In this transect, a variety of climatic conditions are found along an altitudinal gradient. These varying factors are reflected in the presence of six vegetational zones. The analysis of the relation of faunal distribution to vegetation zones along this transect forms a basis for attacking the question posed above.

Description of the Study Area

Physiography.—Three mountain ranges bisect the country of Costa Rica in a northeast to southwest direction: the Cordillera de Talamanca in the southern portion of Costa Rica; the Cordillera Central in the central part of the country; and the Cordillera de Guanacaste in the north. A northern spur of the Cordillera Central, the Cordillera de Tilarán, extends to the northeast from about long 84°30′ W to the southwestern end of the Cordillera de Guanacaste. The average altitude of the Cordillera de Tilarán is 1000 m. The transect, including mountains, lowlands, and Atlantic and Pacific versants, was taken across the northern end of the Cordillera de Tilarán (Fig. 1).

Important towns in the study region include Cañas, Tilarán, and Arenal (Fig. 2). Cañas, located on the Inter-American Highway, is a Pacific coastal lowlands town. Arenal and Tilarán are situated at comparable altitudes on opposite sides of the Cordillera de Tilarán. The study transect was arbitrarily selected as a west to east straight line, 25 km transect through the Cordillera de Tilarán between Cañas and Arenal. The altitude along the transect varies from 88 to 850 m (Fig. 3).

The original forest of the region around Cañas is almost entirely destroyed, and the area is either pasture or land cultivated for cotton production. The area about the town of Los Angeles is also deforested, but the soil is rich compared to that of Cañas, and there are isolated pockets of original forest nearby. Cattle raising is one of the main industries of Tilarán, and pastures predominate. The coffee orchards in the area have the primary forest understories cleared, with the original forest upperstory left as shade for coffee. The Finca El Silencio is situated on the Atlantic-Pacific divide. The drainage for all the Silencio localities is Pacific, and primary forest is abundant. The main product of the finca is cattle. Subsidiary products include corn, beans, and coffee. Finca San Bosco is on the Atlantic slope. The finca is devoted to raising dairy cattle; some plantains are also grown. A primary forest occurs at the 700 m level of the finca. In the vicinity of Arenal, some primary forest is found chiefly along streams. Arenal is a center of cheese production.

Climate.—Within Costa Rica the climatic differences are due primarily to rainfall differences. The greater part of the country is below the frost line. Rainfall patterns for the country are complex, and differ significantly on the two coasts (Coen, 1953).

The northwest portion of Costa Rica that surrounds the transect is marked by three climatic zones; dry, wet with monsoon influence, and wet. The transect itself is marked by varying rainfall and temperature (Fig. 4). The dry zone around Cañas is characterized by four or five consecutive dry months

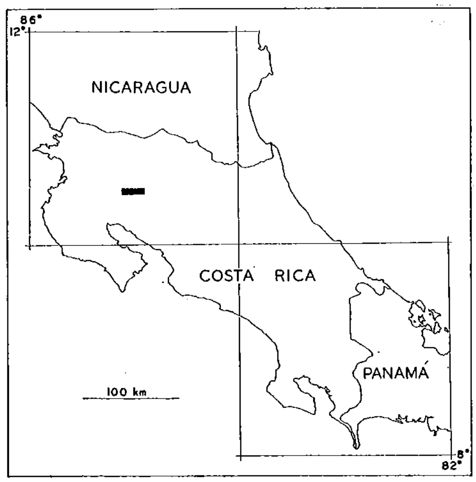

Fig. 1. Map of Costa Rica. Solid bar = transect area.

per year. The monsoon wet zone around Tilarán is characterized by a year-round distribution of rain with a distinct drop in rainfall in the months of January, February, March, and April. During this time, rainfall is sufficient for continuous plant growth. The wet zone around Arenal is limited to below 600 meters in altitude, and is characterized by one dry year every five, approximately. In the dry years, rainfall is reduced in March or April, rarely in September (Coen, 1953). Finca Silencio, located near the top of the Cordillera de Tilarán, also receives the Caribbean moisture as a fine persistent rain.

Vegetation.—Holdridge (1964) devised a three-dimensional system of classification of bioclimates on a world-wide scale by using parameters of temperature, precipitation, evapotranspiration, latitude, day length, seasonal variations of radiation, and atmospheric pressure. Each of the bioclimates supports a distinctive vegetation, and the bioclimates are named by the associated vegetational zone. The bioclimates of Holdridge are used synonymously in the transect with the life zone as defined in the introduction.

The vegetational zones found in the transect from Cañas to Arenal (Tosi, 1965) are as follows: Tropical Dry Forest, Subtropical Moist Forest, Tropical Moist Forest, Subtropical Wet Forest, Subtropical Rain Forest, and Tropical Wet Forest (Fig. 6). The forests range in height from 20 to 45 m and are composed of either three or four stories.

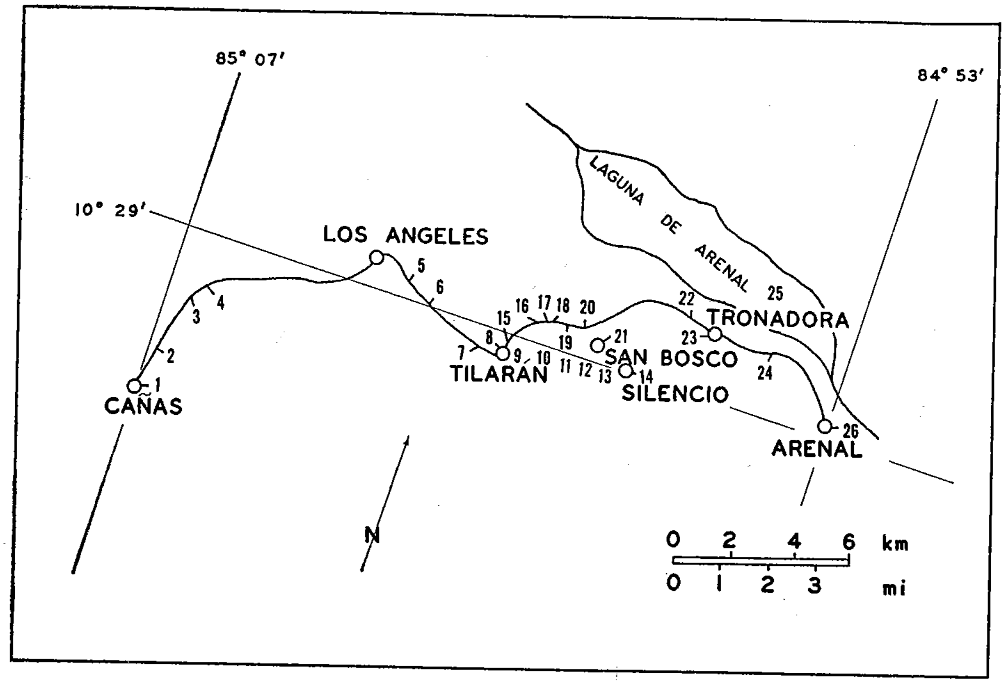

Fig. 2. Detailed map of transect showing principal towns, fincas, and collecting sites (see text). Area shown corresponds with solid bar of Fig. 1.

The Tropical Dry Forest is a deciduous forest, dormant in the dry season. Little original forest remains in the study area. Habitats from which amphibians and reptiles were collected include pastures, ponds (probably temporary), and paved roads. Specimens collected in pastures were associated with exfoliaceous rock, under debris, or in the open pasture. Ponds proved most productive for frogs and frog-eating snakes. Many snakes and frogs were collected on the paved roads at night. Collecting in the forest itself yielded only *Anolis*, *Phyllodactylus*, and *Sceloporus*, which were on the trunks of living or fallen trees.

The evergreen Subtropical Moist Forest is almost nonexistent in the study area, having been removed by human activity. No collecting was done in this zone.

The Tropical Moist Forest is an evergreen forest. The original fourth story of the forest is utilized for shade for the coffee plants in some localities in this zone. Lizards and snakes were found active on the ground, in the ground litter, or concealed under chunks of wood on the ground within this modified forest. Temporary or permanent ponds yielded a number of frogs. Streams in this zone proved to be good collecting sites for frogs, lizards, and snakes.

Stands of the original Subtropical Rain Forest are abundant along the transect. In addition to all the habitat types mentioned for the Tropical Moist Forest Zone, logs found both in pastures and on the forest floor yielded some of the rarer species, and large bromeliads in the trees yielded snakes, lizards, and frogs.

Extensive growths of bromeliads of the Spanish moss type hang from the branches of trees of the Tropical Wet Forest. The habitat types found in this zone are similar to those of the Tropical Moist Forest Zone. A small lake provided an additional habitat.

Materials and Methods

Dunn studied a collection of amphibians and reptiles from Tilarán in the 1930's; Taylor and Pacheco collected there in the summer of 1954 (Taylor, 1955), principally around Pacheco's Finca San Bosco, a few km northeast of Tilarán; William A. Bussing, Jay M. Savage, and Charles F. Walker collected in the Tilarán area in August 1961; Allan A. Schoenherr collected specimens from the area in July 1962; Jay M. Savage and Norman J. Scott, Jr. visited the Tilarán area in August 1963; Scott returned in December 1963, and collected at Finca Silencio, east of Tilarán; Savage and a group of students worked the Cañas area in July 1965. Materials from the 1961–1965 collections are all in the collection of the University of Southern California.

Following the suggestion that a transect study based on an intensive herpetological collection might provide insight into the problems concerning the correlation of faunal distribution with vegetational zones, my wife and I and other workers collected in the area from 24 June to 15 August in the rainy season of 1964.

Specimens forming the basis of the report are located in the following collection: University of Southern California; University of Kansas Natural History Museum; University of Michigan Museum of Zoology; American Museum of Natural History; Museum of Comparative Zoology, Harvard University; United States National Museum; Academy of Natural Sciences, Philadelphia. A private collection from the Tilarán area belonging to Sr. Carlos Enrique Valerio was also examined.

The 26 localities representing all the collecting sites along the transect are presented in an Appendix (see footnote, p. 259) and are shown in Fig. 2.

The distribution of each of the 136 species, represented by 1929 individuals, was mapped, and the number of specimens of each species taken at each site was noted. The raw distributional data are presented in an Appendix (see footnote, p. 259). A preliminary analysis of the distributions indicated that large samples were available for Cañas, Tilarán, Silencio, San Bosco, and Arenal, and fair to poor samples were available for the remaining 21 collecting sites.

The environs of Cañas, as previously stated, are cultivated heavily and little forest now occurs in the area. Cañas lies within a vegetational zone that extends to the north and south for some distance. The amphibians and reptiles collected 10 miles north and south of Cañas were considered to represent forms typical for Cañas before deforestation. All such records were included as from Cañas.

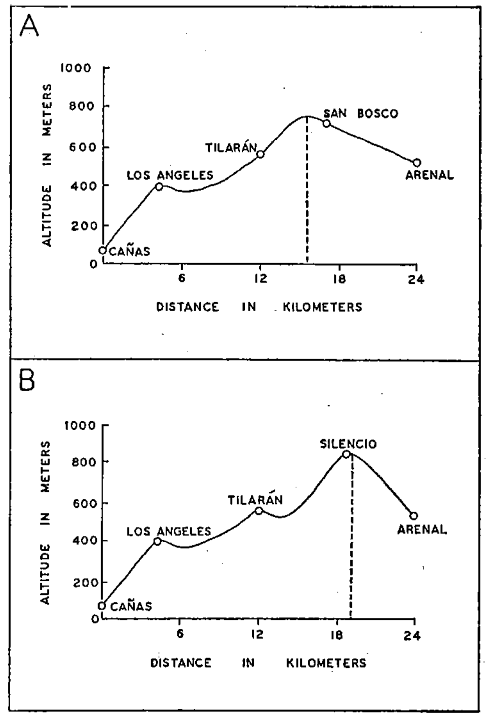

Fig. 3. Altitudinal road profiles of transect: A. through San Bosco; B. through Silencio. Dashed line = continental divide.

Herpetofaunal Assemblages

Herpetofaunal assemblages are defined as groups of species of amphibians and reptiles occurring in a particular area at a particular time. Any one species may be a component of more than one herpetofaunal assemblage.

Most previous workers have differentiated faunal assemblages on the basis of presence or absence of groups of species, endemic species, relative abundance of species, etc. Workers who have utilized this approach include Brown and Alcala (1961), Carriker (1910), Chapman (1917), Duellman (1960), Slud (1964), and Stuart (1950, 1954).

A comparatively recent trend in delimiting faunal assemblages has been a more statistical one. By this method, previously defined groups can be mathematically compared in order to determine the similarity or degree of difference between units, thus allowing the results of various authors to be accurately compared. Workers who have used this approach include Duellman (1963), Hagmeier and Stults (1964), Savage (1960), and Wake (1964).

Simpson (1960) reviewed the mathematical formulae that have been utilized in de-

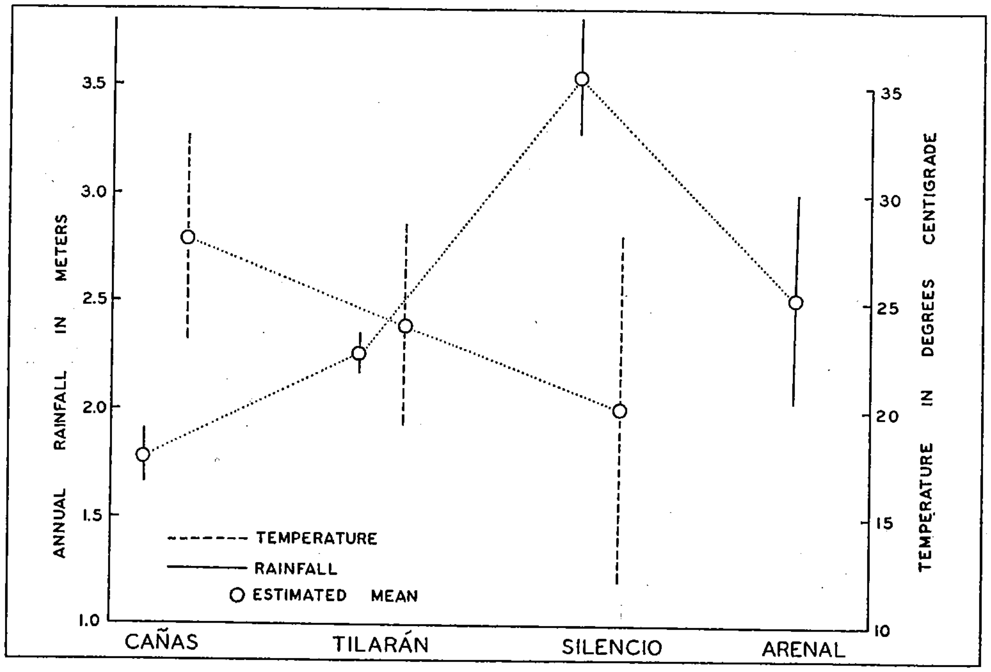

Fig. 4. Rainfall and temperature data for selected stations along the transect. Estimated means connected by dotted line. Data are from: Leon, 1952; Sandner, 1962; Servicio Meteorológico, 1961.

termining the degree of faunal resemblance between samples. He found the best formula for general use to be $C/N_1 \times 100$ where C = the number of taxa common to both samples, and N_1 = the total taxa in the first sample. The purpose of applying this formula to two different samples is to determine the degree of relationship between the samples. Thus if the value obtained is 95, the samples being compared are considered to be closely related; in fact almost identical. Conversely, a value of 10 would indicate a very distant relationship between the samples tested. Savage (1960) took the reciprocal of this formula and derived the Coefficient of Difference (C.D.) $= 1 - C/N_2 \times 100\%$ (N_2 = the total number of species in the larger of the two samples). A C.D. value of 50% or greater indicates the samples being compared are distinct herpetofaunas.

Application of the C.D. formula to the five key locality samples yielded the following. Between samples 1 (Cañas) and 8 (Tilarán), C.D. = 73%; between samples 8 and 14 (Silencio), C.D. = 60%; between samples 14 and 21 (San Bosco), C.D. =45%; and between 21 and 26 (Arenal), C.D.= 69%.

The analyses of these data suggest the presence of four distinct herpetofaunal assemblages along the transect. The C.D. value of 45% between Silencio and San Bosco is relatively high, but in relation to the other samples tested is quite low, and the two samples are considered to be representative of a common herpetofaunal assemblage.

Another method was used in order to test this concept and to determine the geographic extent of the herpetofaunal assemblages along the transect. As the major emphasis of collecting had been at five localities, it was assumed that any species found at any two adjacent major sites (1, 8, 14, 21, 26) would be found between those localities. The total distributional data was transcribed on a large sheet of paper. On this master chart, bars were used to connect localities separated by not more than six localities. The number six was chosen because it was the highest number of localities separating any of the five key localities.

The completed chart demonstrated the presence of 13 major patterns of distribution along the transect. In order to determine the geographic extent of each of the four

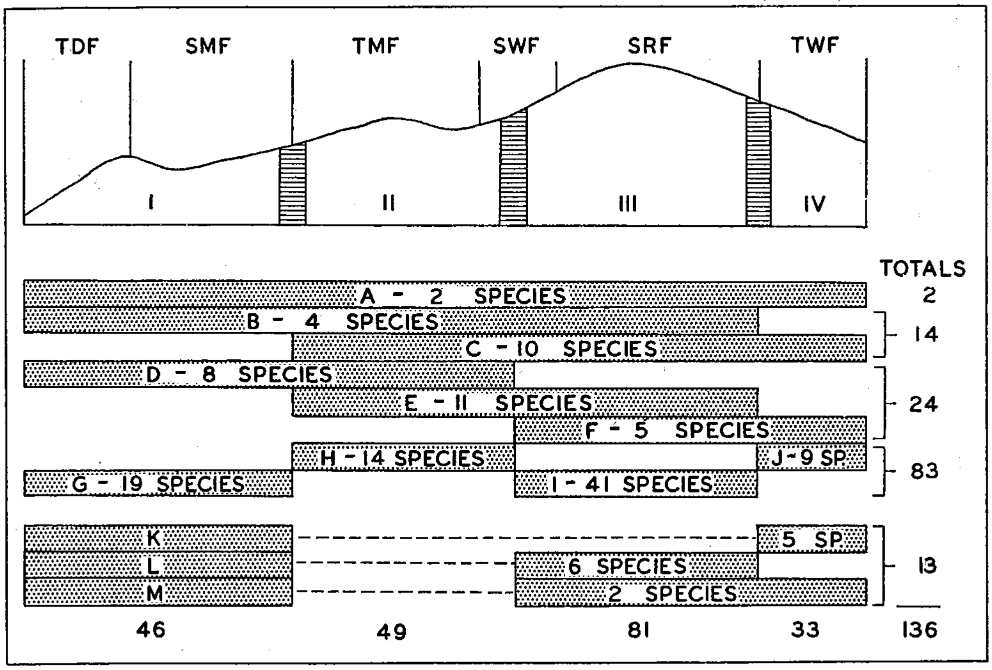

Fig. 5. Summary of herpetofaunal distribution patterns along the transect. Diagrammatic representation of transect at top of figure. Above transect cross section, boundaries between vegetation zones are indicated by vertical lines, and vegetation zones are: TDF = Tropical Dry Forest, SMF = Subtropical Moist Forest, TMF = Tropical Moist Forest, SWF = Subtropical Wet Forest, SRF = Subtropical Rain Forest, TWF = Tropical Wet Forest. Vertical bars (hatching) in the cross section indicate the zones of greatest herpetofaunal change. Patterns of distribution within herpetofaunal zones I–IV are shown below cross section. Within each horizontal bar the number of species representative of a particular pattern of distribution is noted.

herpetofaunal assemblages, the areas of greatest faunal change were tabulated from the master chart. The greater changes occurred between stations 4 and 5, between Cañas and Tilarán; 8 and 11, 16 and 17, between Tilarán and San Bosco-Silencio; and 21 and 22, between San Bosco-Silencio and Arenal. The distributional patterns of the four herpetofaunal assemblages are summarized in Fig. 5.

Lack of data from the Subtropical Moist Forest Zone introduces a margin of error into the analysis. Further collecting and analysis in this zone could conceivably demonstrate the presence of a fifth herpetofaunal assemblage corresponding in distribution with the Subtropical Moist Forest. On the basis of samplings in other areas of Costa Rica, however, the Subtropical Moist Forest is usually inhabited by a fauna similar to that of the Tropical Dry Forest.

The four zones that support distinctive herpetofaunal assemblages center about various locales along the transect as follows: Zone I extends from Cañas almost to Los Angeles, Zone II includes the environs of Los Angeles and Tilarán, Zone III includes the fincas Silencio and San Bosco, Zone IV extends from Tronadora to Arenal. A transect cannot demonstrate zonation. Samples from localities northwest and southeast of the transect indicate that the herpetofauna is distributed zonally along the slopes of the Cordillera de Tilarán, however. The composition of each of the herpetofaunal assemblages is listed in Table 1. Under each assemblage, the presence of a species is indicated by the number of specimens on which the analysis was based.

Vegetation and Herpetofaunal Distribution

At this point it is appropriate to analyze the relationship between the four herpetofaunal assemblages and the six ecologic life zones as defined or characterized by altitu-

TABLE 1. COMPOSITION OF THE HERPETOFAUNAL ASSEMBLAGES.

	Assemblage I	II	III	IV		Assemblage I	II	III	IV
Gymnopis					*L. melanonotus*	1	8	25	30
multiplicata		2	6		*L. pentadactylus*		2	3	
Bolitoglossa sp.			1		*L. poecilochilus*				2
B. striatula			22	19	*Glossostoma*				
Oedipina sp.		3	60	1	*aterrimum*			3	
O. uniformis			2		*Hypopachus*				
Bufo coccifer	14	4	11	2	*variolosus*			41	
B. coniferus			42		*Rana palmipes*	3	1		5
B. haematiticus	1	33	1		*R. pipiens*	3	5	22	
B. leutkenii	3				*R. war-*				
B. marinus		8	13	4	*schewitschii*		2	27	
B. melanochloris				1	*Chelydra*				
Centrolenella					*acutirostris*	1		1	3
albomaculata		6			*Rhinoclemys*				
C. granulosa				1	*annulata*			1	
C. prosoblepon			1		*R. funerea*				1
"Cochranella"					*R. pulcherrima*	2			
fleischmanni		7	1		*Kinosternon*				
Hyla boulengeri			1	5	*leucostomum*			7	7
H. ebraccata		77	97	1	*K. scorpioides*	6			1
H. elaeochroa			9		*Coleonyx*				
H. loquax		4	100		*mitratus*	2	1		
H. microcephala		4	11	2	*Gonatodes*				
H. phlebodes		5	14	19	*albigularis*	1			
H. rufioculis			34		*Lepidoblepharus*				
H. staufferi	1	2			*xanthostigma*		1	28	
H. uranochroa			1		*Phyllodactylus*				
Phyllomedusa					*tuberculosus*	3	5		
annae			3		*Sphaerodactylus*				
P. callidryas		3	113		*lineolatus*			1	
P. saltator			13		*Anolis*				
Smilisca baudinii	3		7		*biporcatus*		4	5	8
S. phaeota	1		7	5	*A. capito*			3	
S. puma				2	*A. cupreus*	4	17	18	1
S. sordida	12	19			*A. humilis*		2	43	
Eleutherodacty-					*A. lemurinus*			1	
lus biporcatus			5		*A. limifrons*			27	8
E. bransfordi		5	111	3	*A. lionotus*		7	42	
E. cerasinus			2		*A. pentaprion*	1			
E. crassidigitus			4		*Basiliscus*				
E. cruentus			4		*basiliscus*		4		
E. diastema			2	1	*B. plumifrons*				3
E. fitzingeri	2	14	5	2	*Corytophanes*				
E. fleischmanni	1	41	59		*cristatus*		2	2	
E. gollmeri			1		*Ctenosaura*				
E. mimus			7		*similis*	4	7		
E. noblei			3		*Iguana iguana*	1			2
E. ridens		5	66		*Polychrus*				
Engystomops					*gutturosus*		1		
pustulosus	4	12			*Sceloporus*				
Leptodactylus					*variabilis*	1	1		
insularum	3				*Leiolopisma*				
L. labialis	3		24	2	*cherrei*		2	38	3

TABLE 1. *Continued.*

	Assemblage I	II	III	IV		Assemblage I	II	III	IV
Mabuya					*L. nigrofasciata*	2			
unimarginata	4	13	1		*L. septen-*				
Ameiva festiva		1	11	12	*trionalis*			2	
A. undulata		11	1	2	*Leptodrymus*				
Anadia metallica			3		*pulcherrimus*	3	1		
Cnemidophorus					*Leptophis*				
deppei	8				*ahaetulla*		2	2	2
Gymnopthalmus					*L. mexicanus*		1	3	
speciosus		3			*Ninia sebae*	1	1		
Lepidophyma					*N. tessellata*			1	
flavimaculatum		1	2		*Oxybelis aeneus*	1	1	1	
Boa constrictor			3		*Pliocercus*				
Epicrates					*euryzonus*			2	
cenchris	1				*Pseustes*				
Loxocemus					*poecilonotus*			1	
bicolor	2				*P. shropshirei*		1		
Chironius					*Rhadinaea*				
grandisquamis			2		*decorata*		1		
Coluber					*Sibon*				
mentovarius	1				*anthracops*	1			
Coniophanes					*S. nebulata*			1	
fissidens		1	1		*Spilotes pullatus*			1	
C. piceivittis		1			*Stenorrhina*				
Conophis					*freminvilli*	2			
lineatus		1			*Tantilla*				
C. nevermanni	2				*annulata*			2	
Dendrophidion					*T. armillata*	1	1		
percarinatus			1		*Trimorphodon*				
Dryadophis					*biscutatus*	3	2		
melanolomus		1	1	1	*Xenodon*				
Drymarchon					*bertholdi*		1		
corais		1		1	*X. rabdo-*				
Drymobius					*cephalus*				1
margaritiferus		3			*Micrurus*				
Enulius					*nigrocinctus*			3	
flavitorques	1				*Leptotyphlops*				
Erythrolamprus					*ater*	2			
bizonus		1	2	2	*Anomalepis*				
Geophis					*dentatus*		1		
hoffmanni		1			*Bothrops atrox*				1
Hydromorphus					*B. nasuta*		4	2	
concolor				1	*B. ophryomegas*	2			
Imantodes					*B. picadoi*		2		
cenchoa			3		*B. schlegelii*		5	1	1
Leptodeira					Total				
annulata	3	1			species 136	44	65	82	39

dinal belts, climatic parameters, and vegetation.

By viewing the distribution patterns of the 136 species within the vegetation zones along the transect, it is quite clear that the distribution of the fauna by vegetation zones demonstrates the same pattern as the distribution within the herpetofaunal zones.

The comparison of the distribution of the herpetofaunal assemblages and vegetational

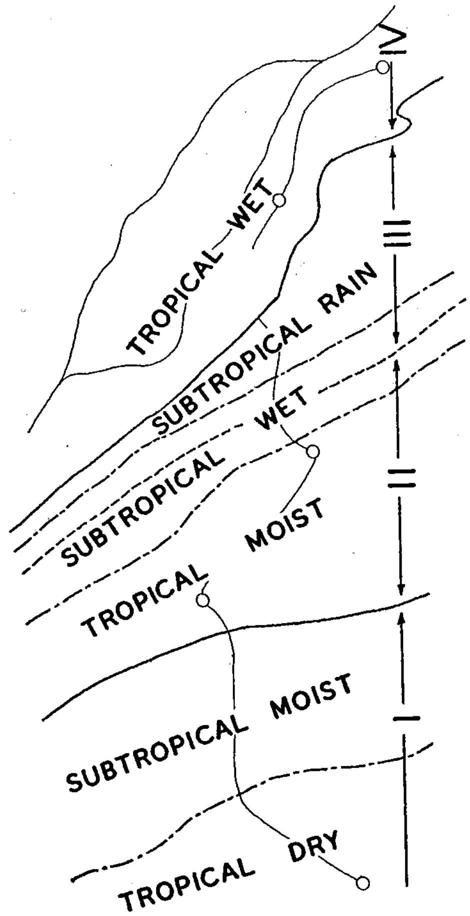

Fig. 6. Comparison of the distribution of herpetofaunal assemblages and vegetation zones. Roman numerals = herpetofaunal assemblages. Solid line = both vegetation and herpetofaunal zone boundary line, dashed and dotted line = vegetation zone boundary line, dashed line = herpetofaunal zone boundary.

zones shows a very close correlation (Fig. 6). One distinct herpetofaunal assemblage is found in the area around Cañas, incorporating the areas which are characterized by the Tropical Dry Forest and Subtropical Moist Forest zones. A second herpetofaunal assemblage is found in the Tilarán area, including the Tropical Moist Forest and a portion of the Subtropical Wet Forest zones. A third herpetofaunal assemblage is found in the area characterized by the remaining portion of the Subtropical Wet Forest and the Subtropical Rain Forest zones. The last herpetofaunal assemblage within the transect is in the area around Arenal, where the Tropical Wet Forest vegetation is characteristic. The Subtropical Moist Forest and Subtropical Wet Forest seem to be intermediate with regard to the distribution of herpetofaunal assemblages.

The distribution of the herpetofaunal assemblages in the transect seems clearly correlated with the ecologic limits of the major vegetation zones. However, several previous studies have demonstrated that herpetofaunal assemblages may be associated with other factors. It is thus necessary to make certain that the observed differences are not influenced by altitude or effects of location in Atlantic or Pacific drainages.

Martin's publication (1958) showed that the distribution of herpetofaunal assemblages in Tamaulipas, México is correlated with altitudinal zones. One assemblage was distributed at essentially the same altitude on either side of the mountain comprising his transect, although the species involved tended to occur at a lower elevation on the eastern slope. The method of checking the effects of altitudinal zonation in the present study is straight-forward. The towns (and immediate environs) of Tilarán (Tropical Moist Forest) and Arenal (Tropical Wet Forest) lie at comparable elevations. The Cordillera de Tilarán lies between these two localities and produces conditions similar to Martin's study area in Tamaulipas. The herpetofaunal samples from the two Costa Rican stations were compared by using the C.D. formula. The Tilarán sample is composed of 45 species and 31 species are represented in the Arenal sample. The C.D. value obtained from the comparison of the two samples is 73%; the samples appear to be from different assemblages. Therefore, different assemblages occur at comparable altitudes on either side of the Cordillera de Tilarán, a situation which contrasts somewhat with the Tamaulipas transect.

Two large samples from the same vegetation zone but from different versants were tested with the C.D. formula in order to determine the effect of Atlantic–Pacific slope differences. The localities are Finca San Bosco (Atlantic slope) and Finca Silencio (Pacific slope) both in the Subtropical Rain Forest Zone, with 52 and 59 species comprising the respective samples. The C.D. value obtained from the comparison was 45%; the samples may be considered as derived from the same faunal assemblage. The usual importance of Atlantic–Pacific slope differences is that different environmental conditions are often associated with the two versants. These differences may be associated with different herpetofaunal associations, but in areas where there are no significant differences in environmental conditions (present study area) the continental divide does not act as an ecologic or geographic barrier.

It is interesting to consider why the herpetofauna is distributed as it is along the transect. As no actual experimentation has been done in the transect area to test the role that ecologic factors play in limiting species distribution, the discussion that follows is solely based upon observations and impressions gained while I was in the transect area. The relationship of herpetofaunal distribution with vegetation zones is usually not a faunal–floral relationship. Only one species seemed to show a distribution correlating with a certain species of plant (*Anadia metallica*, with large tank bromeliads). Many species seemed to depend more on the microhabitat types that were associated with the different vegetations. Thus certain arboreal species that were collected in the transect area came only from the Subtropical Rain Forest, which was the only vegetation with a well developed aerial swamp. Other species appeared to be limited directly by climatic factors. *Rana warschewitschii* was found all over the forest floor in the Subtropical Rain Forest, and only along streams in the other forest zones in which it was collected. As *R. warschewitschii* was not collected in the drier habitats, it would appear that air moisture is a limiting factor in the distribution of this species. Other species seemed to require several hours of solar radiation contact every day. Basking lizards (particularly *Ctenosaura similis*) were common in the Tropical Dry Forest Zone, present in the Tropical Moist Forest Zone, and absent in the Tropical and Subtropical Wet and Rain Forest zones. The climatic factors which affect the distributions of these latter species are for the most part modified by the vegetation in any area.

It is difficult to imagine the presence of 136 species of amphibians and reptiles along a 25 km transect. The length of the transect is marked by moderate changes in elevation, temperature, and rainfall. The total difference of elevation is 780 m; the temperature ranges from 12 to 33° C; and the rainfall ranges from 1700 to 3800 mm/year. Yet within this short distance, marked by these differences, six distinct vegetation formations and four distinct herpetofaunal assemblages are found.

The results of the present analysis contrast markedly with certain aspects of Grinnell and Storer's (1924) classic study of the animal life in the Yosemite area. The extratropical Yosemite transect was 90 miles (145 km) in length, the total difference in elevation within the transect was about 3850 m, and 27 species of amphibians and reptiles were collected from the transect area. Roughly speaking, the Yosemite transect was six times as long, five times as high, and contained one-fifth the herpetofauna of the tropical Tilarán transect. Both transects cut across six life zones. Grinnell and Storer found that the life zones were not sharply defined; there was a wide area of faunal overlap between adjoining zones. This contrasts to the sharply defined faunal zones found in the Tilarán transect. Whereas the zones of faunal overlap between life zones in the Yosemite transect was in terms of many miles, the zone of faunal overlap in the Tilarán transect is in terms of a few km. Grinnell and Storer also state a "well established law" that if zones are telescoped together, their boundaries are lost, and the zones so affected are fused. The Tilarán transect was purposely taken in an area where the life zones were telescoped to a great degree. Rather than a fusion of life zones, the Tilarán transect demonstrated that the life zones and particularly the distribution of herpetofaunal assemblages are sharply defined. The relative abundance and distributional patterns of the ectothermic amphibians and reptiles, the compaction of life zones in tropical areas, and the sharp definition of these zones in tropical areas all reflect the ecologic differences between the tropical Tilarán and extratropical Yosemite transects. But more importantly, from this analysis the life zone appears to be as valid an ecologic concept in the tropics as in the extratropics.

Stuart (1950, 1955, 1964) questioned the validity of relating biotic areas with life zones; in other words he minimized the importance of present day ecological parameters in the dispersal of faunal groups. The present analysis points out the important influence of ecologic parameters in limiting the distribution of amphibians and reptiles in the transect area in northern Costa Rica. It is assumed that the same type of analysis in any other local tropical area would yield similar results. It is probable that the integral relationship of ecologic factors and faunal distribution has been maintained for a considerable period in history, and that ecologic parameters have been an important influence in the dispersal of faunal groups. There is, in conclusion, an interdependent relationship between life zones, biotic areas, and faunal distribution patterns.

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