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Variation in altitudinal populations of the salamander, Bolitoglossa subpalmata, on the Cerro de la Muerte, Costa Rica

by

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The tropical plethodontid salamander, *Bolitoglossa subpalmata,* is well known for the striking variation it exhibits in color and pattern. Comments on this variability were included in the original description by BOULENGER (1) and later by DUNN (2). TAYLOR (6) noted the general types of coloration present in the species and also described two closely related forms, *B. torresi* and *B. pesrubra.* Subsequent studies by WAKE and BRAME (8) and myself (7) pointed out that Taylor's descriptions were actually based upon variants of *B. subpalmata.*

During my research on the ecology of *B. subpalmata* in Costa Rica I had the opportunity to examine specimens collected throughout the more than 750 m (2,460 ft.) of elevation over which the species occurs in the Cerro de la Muerte (Cerro Buena Vista) in the Cordillera de Talamanca. The present study is an attempt to analyze color, pattern and size variation in altitudinal populations of *B. subpalmata* in this region.

METHODS AND MATERIAL

In the vicinity of the Inter-American Higway, which transects the Cerro de la Muerte, quadrat samples consisting of 187 specimens were collected at vertical intervals of 150 m between the lowest elevation commonly occupied by the species (2,450 m) and the summit area (3,200 m).

Color and pattern of living specimens were numerically scaled on the basis of standards established by preliminary inspection of a large series. The terminology of HERTZLER (4) has been adopted for the classification of chrom-

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atophores. Melanophores, erythrophores (lipophores) and iridophores (guanophores) on the dorsum (posterior to second costal groove from axilla), gular region, left forelimb and venter (anterior to second costal groove from groin) were assigned values by comparison with the scales shown in Fig. 1. Entire surfaces of the limb and the gular region were included. Because of the generally repetitive character of dorsal as well as ventral patterns, each was classified on the basis of only two costal folds. Using zero to indicate absence of a chromatophore type, the concentration indices increase toward complete suffusion. Gular and ventral patterns were scaled from 0 to 7. The greater variation exhibited on the dorsum made necessary a range of 0 — 8. As there is a tendency for the distribution of one kind of chromatophore to be interrupted or masked by the presence of another, melanophore concentration index can frequently be used as the reciprocal of indices for erythrophores and iridophores, however in some animals the absence of melanophores results in localized unpigmented areas.

Examination of chromatophore distribution was made under 20× magnification. Measurements of standard length (snout - posterior margin of vent) were taken from a separate series, totalling 344 adults, to the nearest 0.1 mm on specimens relaxed in chlorobutanol. Repeated measurements indicate an accuracy of ± 0.2 mm. Specimens obtained from this study are catalogued in the University of Southern California Costa Rican series (USC - CR).

RESULTS

The numerical scales established in Fig. 1 provide a basis for statistical evaluation of chromatophore distribution in the separate samples. Averages of concentration indices for melanophores, erythrophores and iridophores observed on the described body parts for each altitudinal sample are graphically presented in Figs. 2, 3 and 4.

DORSUM: Means of dorsal melanophore concentration range from 2.88 ± 0.22 (standard error) at the highest elevation (3,200 m) to 6.14 ± 0.35 in the 2,900 m sample. Average index for the entire series is 4.59 ± 0.31. Dorsal erythrophores demonstrate a range of from 0.24 ± 0.09, at 3,050 m to 2.40 ± 0.55 at 2,450 m, with a mean index for all samples in 1.30 ± 0.41. Extremes of iridophore concentration are from 2.19 ± 0.30 at 2,750 m to 5.96 ± 0.18 at the summit; average for all specimens is 3.78 ± 0.47.

FORELIMB: Melanophore concentration is conspicuously dominant (5.20 ± 0.30) in the lowest elevation and least (1.52 ± 0.001) at the summit, with an overall index of 3.49 ± 0.24. The reverse situation is shown by erythrophores; only 1.86 ± 0.34 at 2,450 m, but 6.04 ± 0.26 at 3,200 m (average, 4.08 ± 0.41). No iridophores (zero) are present on the forelimbs of any specimens taken at 2,900 m, while those from 2,450 m showed the greatest concentration (2.19 ± 0.33). Mean distribution of forelimb iridophores is 0.80 ± 0.20.

GULAR REGION: Extremes of gular melanophore concentration are between 1.48 ± 0.16 (at 3,200 m) and 5.66 ± 0.26 (at 2,450 m), with an average index of 3.55 ± 0.30. Gular erythrophores range from 0.24 ± 0.13 to 6.00

± 0.35 in the lowest and highest samples, respectively; averaging 3.74 ± 0.44. Iridophores are least frequent in specimens from 2,900 m elevation (0.22 ± 0.16), while those from 2,450 m have the greatest suffusion (2.00 ± 0.22). Average index for gular iridophores is 0.62 ± 0.15.

VENTER: There is relatively slight variation in the occurrence of ventral melanophores. At 3,050 m the sample demonstrates a mean index of 5.28 ± 0.30. A maximum of 6.48 ± 0.24 is shown by the specimens from 2,450 m. Mean index for all samples is 6.02 ± 0.29. The greatest of ventral erythrophore concentration is exhibited by animals from the lowest two quadrats; 0.14 ± 0.11 at 2,450 m to 1.71 ± 0.99 at 2,600 m. Index of ventral erythrophores for all specimens is 0.89 ± 0.30. Iridophores range from 0.24 ± 0.07 at 2,750 m to 1.91 ± 0.21 at 2,450 m, with an overall average of 1.08 ± 0.18.

STANDARD LENGTH: Results of the analysis of standard length in altitudinal samples of adult (> 30.0 mm) *B. subpalmata* are given in Fig. 5 The greatest size variation (from 31.0 to 72.0 mm) occurs in specimens from both 2,750 and 2,900 m, while the least (31.0 — 54.0 mm) is shown in those from 2,600 and 3,050 m. Greatest difference in sample means (10.1 mm) is between salamanders from 2,450 m and those from 2,750 m, while least variation (0.5 mm) is shown between specimens from 2,600 m and 2,750 m.

DISCUSSION AND CONCLUSIONS

Extremes of variation in melanophore concentration indices for different body parts is less than that demonstrated by either erythrophores or iridophores. The least range of melanophore variation is shown on the ventral surface, which is frequently almost uniformly dark, especially in specimens from the lower slopes of the Cerro de la Muerte (See Fig. 2). The gular region is usually darkest in those animals occupying the lower elevations and lightest in those from the summit; however, the reduction in gular melanophores is not shown to be entirely consistent with increasing altitude. Forelimbs are often uniformly black (or dark brown) at the lower limits of the species distribution on the Cerro de la Muerte, while in many of the summit specimens melanophores are completely absent from the appendages. No graduated pattern of dorsal melanophore suffusion is exhibited in the altitudinal samples. Mottling of black or brown occurs in specimens from 2,450 m, but those in the intermediate elevations tend toward greater darkness. Animals from the summit show the greatest tendency for mottling or light dorsal coloring by the reduction of melanophores.

Erythrophores are least apparent in specimens from the lower elevations, as shown in Fig. 3. In all samples these cells are usually reduced in number on the abdominal and dorsal surfaces. However, two of the 187 specimens have a broad, dorsal stripe of brick-red coloring. The limbs, usually dark among the lowest populations, gradually become more reddish with an increase in altitude. The majority of my sample from 3,200 m exhibit uniformly reddish limbs. Also, with some minor erratic variation, the gular region tends to be more reddish in the higher elevations of the mountain.

Iridophores produce an almost iridescent metallic quality of either dull silver or gold appearance; however, the latter coloration does not appear as more than a minute well dispersed flecking in any of my specimens. On the ventral surface flecking or mottling is most frequently present in animals from the lowest as well as the two highest quadrats and only seldom in salamanders from the intermediate levels. Gular iridophores are esentially erratic in their presence among the separate samples, as are those on the limbs. (Refer to Fig. 4). The most striking feature of iridophore distribution can be noted on the dorsum, in which the entire surface, including the tail, may be a uniform dull silver. I have found this coloration to be fairly common among specimens from elevations of more than 3,000 m.

One exceptional case of coloration is worthy of special mention. An adult female from 2,600 m had a broad yellow-white dorsal stripe extending from the nape to the tail, which appared to result from the total absence of chromatophores.

For any chromatophore type the least degree of variation is exhibited below about 2,900 m within the study area and the greatest diversity near the summit. Limbs, and to a lesser degree the gular region, are the only body surfaces showing a generally consistent cline directly correlated woth elevation, in that there is gradual increase in the concentration of erythrophores and a coincident decrease in melanophores. Iridophores, however, are not graduated in this manner.

Size clines, either inverse or direct, have been reported in *Ensatina eschscholtzii* by STEBBINS (5) and *Desmognathus ochrophaeus carolinensis* by HAIRSTON (4). However, by any analysis of the information included in Fig. 5, there is no relation of size and elevation of *Bolitoglossa subpalmata* on the Cerro de la Muerte.

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SUMMARY

Altitudinal populations of the plethodontid salamander, *Bolitoglossa subpalmata,* are quantitatively compared for variation in color, pattern. and size. The greatest diversity in color and pattern occurs at elevations above 2,900 m. Only the limbs and the gular region demonstrate a clinal character, in that they increase in the amount of redness present with higher elevation. No evidence of a size cline, either inverse or direct, has been obtained.

RESUMEN

Se comparan cuantitativamente poblaciones de la salamandra pletodóntida *Bolitoglossa subpalmata* de altitudes diferentes desde su límite inferior a los 2,450 m hasta los 3,200 m, estudiadas a intervalos verticales de 150 m, con respecto a variación de color, diseño de coloración y tamaño. La mayor diversidad de color y diseño se presenta de los 2,900 m para arriba. Sólo las extremidades y la región gular muestran un carácter clinal, en que la proporción de rojo aumenta con la altitud. No se observó ninguna variación clinal, ni directa ni inversa, en el tamaño.

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Fig. 1. Color standards for quantifying concentration and distribution of chromatophores.

Bolitoglossa subpalmata

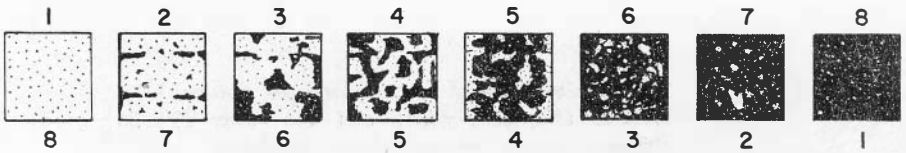
Scales of Pattern and Color Classification

Examination at 20X, 0 = Absence

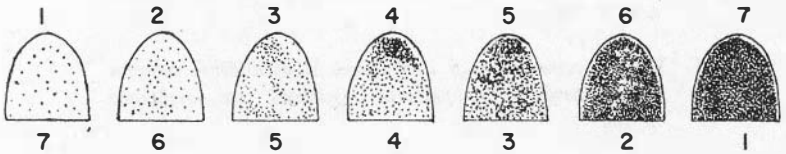
Melanophores ⟶ ⟵ Erythrophores

⟵ Iridophores

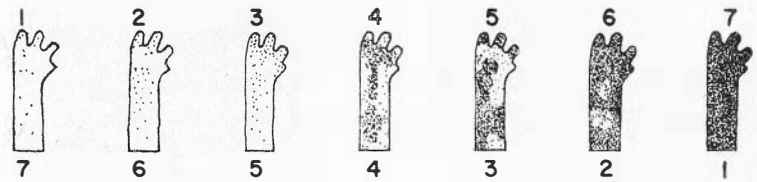
DORSAL PATTERN (2 Costal Folds Behind Axilla)



GULAR PATTERN



LIMB PATTERN (Left Arm)



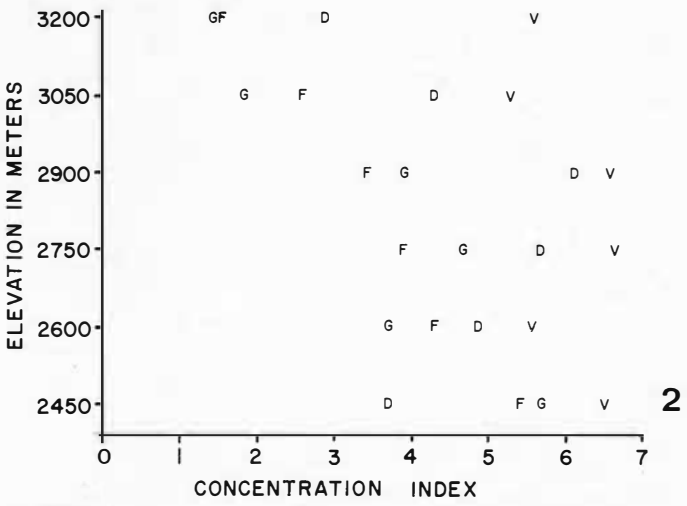
VENTRAL PATTERN (2 Costal Folds Anterior to Groin)

1

Fig. 2. Mean concentration of melanophores on dorsum (D), forelimb (F), gular region (G) and venter (V) in altitudinal samples of *Bolitoglossa subpalmata.*

Fig. 3. Mean concentration of erythrophores in altitudinal samples of *Bolitoglossa subpalmata.* Symbols are explained in Fig. 2.

Fig. 4. Mean concentration of iridophores in altitudinal samples of *Bolitoglossa subpalmata.* Symbols are explained in Fig. 2.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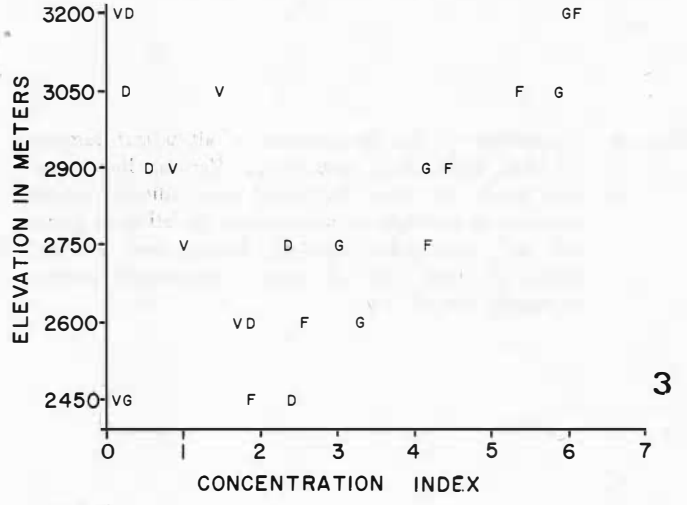
F G D V
F G D V
G F D V
D F G V
0 1 2 3 4 5 6 7
CONCENTRATION INDEX
2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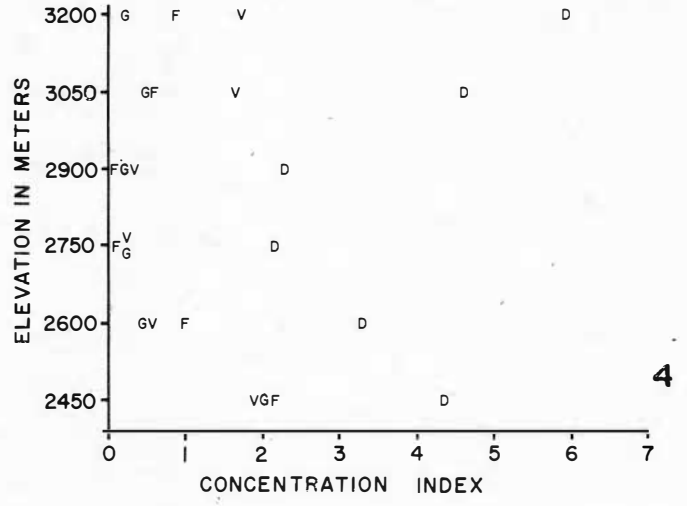
CONCENTRATION INDEX
3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FGV D
V
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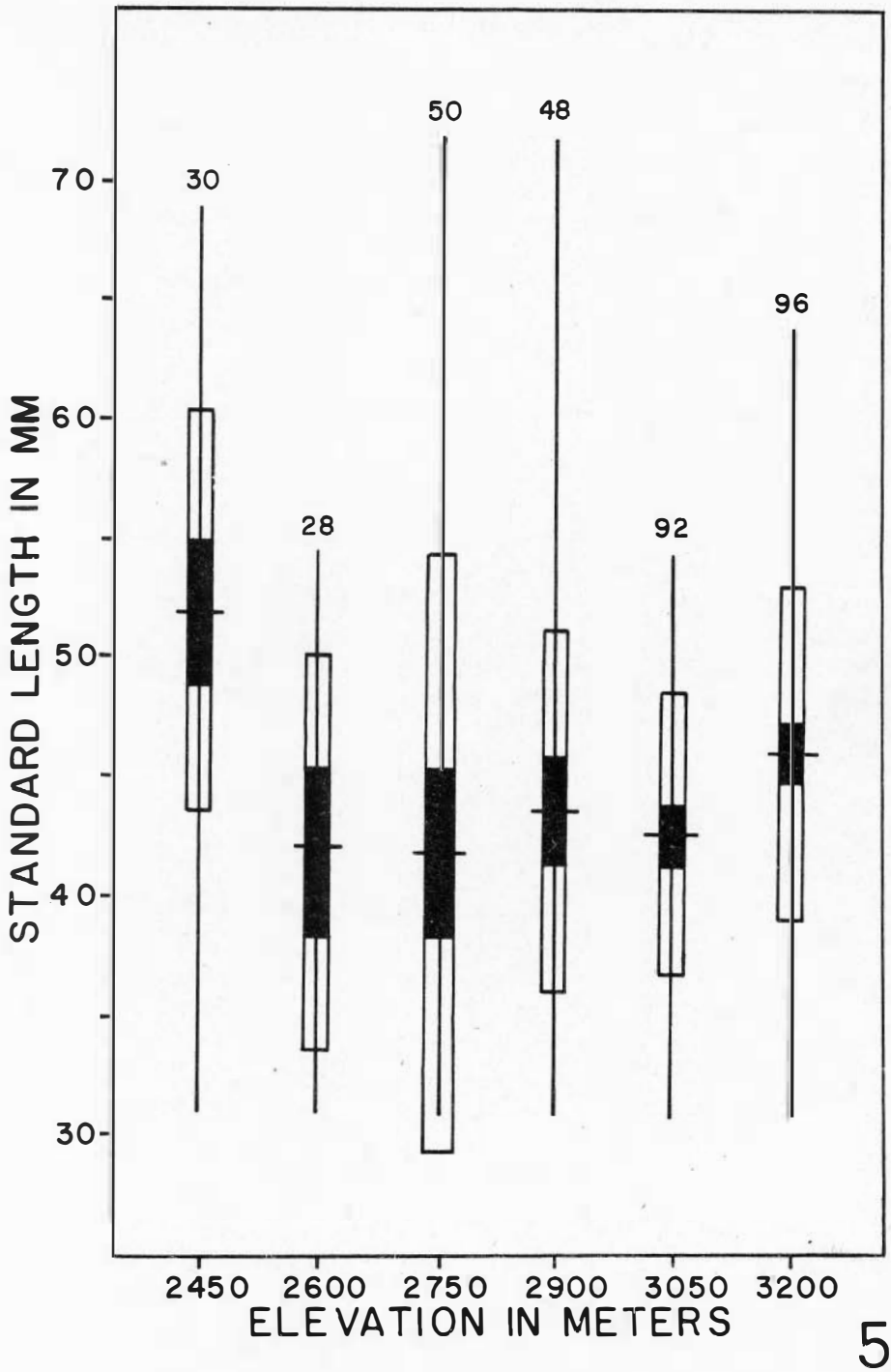
GV F D
VGF D
0 1 2 3 4 5 6 7
CONCENTRATION INDEX
4

Fig. 5. Comparison of size distribution in altitudinal samples of adult *Bolitoglossa subpalmata*. Vertical line represents total size range, horizontal line indicates sample mean, open rectangle is one standard deviation on either side of mean, solid rectangle denotes two standard errors on each side of mean. Superscript number represents sample size.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STANDARD LENGTH IN MM
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ELEVATION IN METERS

5