LETTERS TO THE EDITORS

LATITUDINAL PATTERN OF BETWEEN-ALTITUDE FAUNAL SIMILARITY: MOUNTAINS MIGHT BE "HIGHER" IN THE TROPICS

Moving up or down a mountain from a given site, one encounters faunas that differ by varying degrees. The elevational separation between sites obviously influences the magnitude of that difference (faunal similarity is inversely proportional to elevational separation); local environmental discontinuities, steepness of slope (Beals 1969), and certain global factors may also affect these "between-altitude" faunal similarities. Here I examine one possible global relationship, that of latitude and the extent of faunal similarity for reptilian and amphibian communities at different altitudes. I gathered these data to test Janzen's (1967) hypothesis that mountains are effectively "higher" to animals in the tropics; if this is true, then "between-altitude" faunal similarity should vary directly with latitude.

I first determined the altitudinal distributions of frogs, lizards, and snakes (excluding geckos, aquatic snakes, and fossorial squamates) for nine areas (eight for frogs) from Tilarán, Costa Rica, to Lassen Peak, California. If authors did not list the altitudinal range of a species, I determined it from gazeteers in conjunction with locality data considered valid by the authors.

For each area I then calculated the relative faunal similarity (lizards, snakes, and frogs, separately) between two altitudinal bands (each 200 m wide) separated by 600 m in elevation using Dice's (1945) index: $FS = 2C/(N_1 + N_2)$, where FS = faunal similarity, C = number of shared species, and N_1 and N_2 = number of species in lower and upper zones, respectively. Alternative indices such as $FS = C/(N_1 + N_2 - C)$ from Jaccard (1912) or the resemblance equation of Preston (1962) are strongly correlated with Dice's index (all $r > .98$, from a sample of 10 pairs of arbitrary values), and the relationships are nearly linear. Use of Preston's complex transcendental equation appears, therefore, inefficient. (See Southwood [1966] for discussion of sensitivity of Dice's and Jaccard's indices to sample size.)

For most areas I calculated an average FS ($\overline{FS}$) of three separate comparisons (0–200 m with 801–1,000 m; 401–600 m with 1,201–1,400 m; and 601–800 m with 1,401–1,600 m). Two areas had a total altitudinal range of less than 1,700 m: $\overline{FS}$ for San Jacinto (Atsatt 1913) was determined from the upper two altitudinal comparisons, and FS for Tilarán (Heyer 1967) was determined from the lowest comparison only.

TABLE 1

LATITUDE (N), FAUNAL SIMILARITY $(\overline{FS})$, AND SPECIES DENSITY (SD) FOR LIZARDS, SNAKES, AND FROGS

LOCALITY	LATITUDE	LIZARDS		SNAKES		FROGS		REFERENCE
		$\overline{FS}$	SD	$\overline{FS}$	SD	$\overline{FS}$	SD	
Lassen Peak, Calif.	40.5	.571	7	.637	9	.952	6	Grinnell et al. 1930
Yosemite, Calif.	38	.602	7	.560	10	.841	6	Grinnell and Storer 1924
San Jacinto, Calif.	34	.675	16	.538	16	...	...	Atsatt 1913
Sinaloa, México	25	.530	28	.497	51	.462	31	Hardy and McDiarmid 1969
Gomez Farias, México	23	.498	23	.310	42	.708	20	Martin 1958
Michoacán, México	19	.486	42	.412	69	.605	37	Duellman 1965
Alta Verapaz, Guatamala	15	.324	34	.298	53	.283	28+	Stuart 1948
Santa Marta, Colombia	10.7	.137	18	.589	30	.308	28	Ruthven 1922
Tilarán, Costa Rica	10.5	.125	23	.067	46	.154	49	Heyer 1967

TABLE 2

KENDALL RANK (τ) AND PARTIAL RANK $(\tau_{xy \cdot z})$ CORRELATION COEFFICIENTS FOR
COMPARISONS AMONG $\overline{FS}(Y)$, LATITUDE (X_1), AND SPECIES DENSITY (X_2),
WHERE $YX_1 \cdot X_2 = Y$ vs. X_1, X_2 HELD CONSTANT

Comparison	Lizards	Snakes	Frogs
Y vs. X_1	.833***	.611*	.857**
Y vs. X_2	−.543*	−.556*	−.545*
X_1 vs. X_2	−.457	−.500*	−.545*
$YX_1 \cdot X_2$	.782	.466	.797
$YX_2 \cdot X_1$	−.329	−.380	−.181

* Statistically significant at 5% level.
** Statistically significant at 1% level.
*** Statistically significant at .1% level.

I also recorded the number of species occurring on each area (species density $= SD$) and, when possible (six of nine transects), an index of the thoroughness with which areas were sampled (total specimens in sample/total species). This latter index is of potential interest because the fewer the specimens per species, the lower $\overline{FS}$ may be as a result of sampling error. This index is not, however, correlated with $\overline{FS}$ (Kendall rank tests, all $P > .1$), but data are too few to reject this possible bias with confidence.

Latitude, $\overline{FS}$, SD, and the reference for each area are given in table 1; $\overline{FS}$ is directly correlated with latitude (all $P < .05$) and inversely correlated with SD (all $P < .05$) for all three taxa (table 2). Not surprisingly, latitude and SD are inversely correlated (all $P < .05$) for snakes and frogs and are marginally correlated ($P = .06$) for lizards.

Because of significant correlations between $\overline{FS}$ and both latitude and species density, I further examined these associations using partial correlation analysis. It seems that $\overline{FS}$ is primarily associated with latitude for lizards, snakes, and frogs (table 2).

Low $\overline{FS}$ in the tropics might reflect either a high rate of species dropout with altitude or a high rate of turnover of species. The average ratio of N_2 to N_1 for each transect is not significantly correlated (all $P > .1$) with latitude for these reptiles and amphibians, suggesting that the correlations between $\overline{FS}$ and latitude are primarily a function of species replacement, not species dropout.

Heyer (1967) noted that herpetofaunal zones along an altitudinal transect in Costa Rica were narrower and more sharply defined than those on a similar, temperate zone transect (Yosemite; Grinnell and Storer 1924). Wake and Lynch (1976) found a similar trend with New World salamanders. The present analysis supports the generality of these observations; between-altitude faunal similarity of lizards, snakes, and frogs is less in the tropics.

Interpretation of this pattern is hazardous because overall trends may be obscured by local anomalies, differences in area, or inadequate sampling and because causal factors associated with latitude are likely to be many (Pianka 1966) and their interactions complex. Yet, several possible explanations can be

suggested. First, because interspecific competition can restrict altitudinal ranges of animals (Diamond 1972; Terborg and Weske 1975), the observed correlation between $\overline{FS}$ and latitude might reflect greater competition in the tropics. I cannot evaluate this hypothesis. Second, because the species density of predators (snakes) has been related to the species density of prey (frogs and lizards; Arnold 1972), $\overline{FS}$ of snakes might be related to $\overline{FS}$ of frogs and lizards. However, correlations between these $\overline{FS}$ values are insignificant (all $P > .05$).

Finally, Janzen's (1967) theoretical discussion of effective mountain height at different latitudes is relevant. Noting that climatic variability at a given site is lower in the tropics than in the temperate zones, Janzen proposed that tropical animals might be adapted to relatively narrow ranges of environmental temperatures and observed that two tropical localities on an altitudinal transect overlap less in climatic regimes than two similarly spaced temperate-zone localities. Janzen then speculated that mountains might be effectively "higher" in the tropics because an animal attempting to move up or down a tropical mountain will more likely encounter a climatic regime "to which it is neither acclimated nor evolutionarily adapted" (p. 242).

The observed lower between-altitude faunal similarity (Heyer 1967; Wake and Lynch 1976; this report), while not proving Janzen's hypothesis, is consistent with it. A less blunt approach will be necessary to determine if effective mountain height is truly important and, if so, whether it is directly affecting animal distributions or is indirectly affecting them via vegetational associations (Martin 1958; Duellman 1965; Heyer 1967).

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