

BODY SIZE AND ELEVATION IN NEOTROPICAL SALAMANDERS.—The purpose of this report is to examine several assumptions regarding body size in lungless salamanders, Plethodontidae. Plethodontids as a group commonly are characterized as diminutive. Among tropical plethodontids (Bolitoglossini), species with large adults are often reported to be restricted to high elevations while small species are not. These characterizations lack documentation, and frequently attribution as well. Even so, ecological physiologists have marshalled these assumptions to support hypotheses relating body size, respiratory structure and biogeographic distribution in plethodontids.

For example, Beckenbach (1975) measured differences in critical oxygen tension between large and small plethodontids. These differences indicated that large plethodontids were less able than small plethodontids to supply their tissues with oxygen under experimental conditions. Beckenbach interpreted these data to suggest that gas exchangers of large plethodontids might be inadequate to support the high cellular metabolism engendered by high temperatures characteristically associated with low elevations in the tropics. Accordingly he reasoned that large plethodontids may be restricted to high elevations because temperatures there are cool and oxygen demand would therefore be low. In support of his explanation, Beckenbach noted a positive relationship between body size and elevation in neotropical salamanders.

The suggestion that respiratory considerations limit body size in plethodontids remains

TABLE 1. BODY SIZE AND MINIMUM ELEVATIONAL RANGE IN NEOTROPICAL PLETHODONTID SALAMANDERS. Values are numbers of species in each size-elevation category. Upper number in each cell is number of *Bolitoglossa* species; lower (italicized) number is number of all species in all genera of tropical plethodontids that fall into each cell. Data and categorization are from Wake and Lynch (1976).

Minimum primary elevational range	Typical size of full adult individuals, snout to posterior end of vent			
	0-35 mm	40-55 mm	60-75 mm	>80 mm
0-500 m	2	8	5	7
	2	<i>11</i>	9	<i>8</i>
500-1,500 m	1	12	6	1
	8	<i>19</i>	9	<i>2</i>
1,500-2,500 m	1	8	7	2
	<i>10</i>	<i>15</i>	<i>13</i>	<i>4</i>
Above 2,500 m	0	1	2	1
	6	<i>4</i>	8	<i>1</i>

controversial (Feder, 1978). In this report we take no position regarding this physiological problem. However, we contend that no demonstrable positive correlation exists between body size and elevation in tropical salamanders, and in fact some of the largest tropical plethodontids live at low and moderate elevations. Hence observed trends in body size are inconsistent with respiratory restriction to small size.

We have analyzed the data of Wake and Lynch (1976) for 129 species of neotropical salamanders. Wake and Lynch placed species into four categories each of "typical size of full adult individuals" (hereafter "size") and "primary elevational range" (hereafter "elevation"). In view of limited series for some species, pronounced sexual dimorphism in many species, and evident but uncharacterized intraspecific variation in body size, this categorization is the most accurate assessment of size and elevation for tropical plethodontids realizable at present. We have summarized their data for size and minimum elevation in Table 1.

To assess correlation between size and minimum elevation we used Kendall's tau, a non-

TABLE 2. BODY SIZES OF SOME LARGE BOLITOGLOSSINE SALAMANDERS.

Species and locality	MVZ* catalog number	Elevation (m)	Mass (g)	Length (mm)	
				Snout-vent	Total
<i>Bolitoglossa dofteimi</i>					
San Pedro Sula, Honduras		1,200	39.7	121	
San Pedro Sula, Honduras		1,200	47.1	130	
San Pedro Sula, Honduras		1,200	47.9	125	
Finca El Volcan, 25 km NW Senahu, Alta Verapaz, Guatemala	161645	875	31.9	112	205
Finca El Volcan, 25 km NW Senahu, Alta Verapaz, Guatemala		875	25.4	102	193
<i>Pseudoeurycea bellii</i>					
Las Vigas, Oaxaca, Mexico		2,230	40.8		
3.4 km N Raices, Mexico, Mexico		3,320	58.0		
6.3 km S Putla, Oaxaca, Mexico	106851	730	—	118	238
6.3 km S Putla, Oaxaca, Mexico	137874	730	—	107	221
Base of Cerro Las Viboras, N slope of Nevado de Colima, 23 km W Ciudad Guzman, Jalisco, Mexico	171794	2,219	71.8	143	210
Base of Cerro Las Viboras, N slope of Nevado de Colima, 23 km W Ciudad Guzman, Jalisco, Mexico	171795	2,219	48.0	128	227
Base of Cerro Las Viboras, N slope of Nevado de Colima, 23 km W Ciudad Guzman, Jalisco, Mexico	171796	2,219	41.3	114	211

* Museum of Vertebrate Zoology.

parametric correlation coefficient. Kendall's tau is relatively insensitive to tied ranks (Nie et al., 1975:288), which are common in Table 1. According to this statistic, elevation and size show a small but significant negative correlation for 129 species of neotropical plethodontids ($\tau = -0.131$; one-sided $P = 0.04$). Clearly no positive correlation exists between body size and minimum elevation in tropical plethodontids. In fact, as Table 1 indicates, species that fall in the largest size category are most numerous at low elevations.

We repeated this analysis for the 64 species in the genus *Bolitoglossa*, the most widespread and speciose genus of neotropical plethodontids (Wake and Lynch, 1976). Contrary to Beckenbach's (1975) claim, no positive correlation between size and minimum elevation is evident within this genus ($\tau = -0.022$, one-sided $P = 0.42$).

In view of such misconceptions, it is worth emphasizing how large some neotropical plethodontids become. We report here (Table 2) limited information concerning body size for two of the largest species of tropical salamanders, *Bolitoglossa doleini* and *Pseudoeurycea bellii*. The latter species is the largest tropical salamander, has one of the largest geographical ranges, and has the broadest elevational limits of any salamander in the world. It is no smaller at low than at any other elevational level. Both species achieve exceptionally large body size at elevations below 1,000 m.

Contrary to assertions of exiguity (Rensch, 1959; Schmidt-Nielsen, 1979), these measurements suggest that some neotropical plethodontids are among the largest terrestrial salamander species. Except in the physiological literature, body weight data are available for few salamander species. However, body length data (available in many field guides) together with the scanty weight data provide some basis for comparison of neotropical plethodontids with other salamanders. The largest neotropical plethodontids (Table 2) are larger than most of the terrestrial and semi-terrestrial temperate zone salamander fauna. The only obvious exceptions to this generalization are *Ambystoma tigrinum* and *Dicamptodon ensatus*, two lunged species that may exceed 100 g body weight (Smith and Reese, 1968). Many aquatic urodeles, however, exceed the maximum body size of the terrestrial salamander fauna; e.g. *Ampiuma*, *Andrias*, *Cryptobranchus* and *Siren*.

Beckenbach's (1975) physiological work, based on temperate zone plethodontids under

hypoxic conditions, suggests that lunglessness should limit body size in plethodontids living at warm temperatures. Because the largest plethodontids can be found at elevations below 1,000 m in tropical lowlands, we feel this conclusion bears reexamination. We propose four hypotheses to explain the contradiction between Beckenbach's data and the distribution of large plethodontids: 1) Gas exchange is restricted at high temperatures, but this restriction does not affect organismal function in an ecological sense; 2) Oxygen demand does not exceed the capacity of the gas exchange system in plethodontids, even at high temperatures; 3) Large tropical plethodontids have developed specializations for gas transport; 4) Evidence derived from experimentation under hypoxia cannot be extrapolated to field conditions. We hope that this report will stimulate examination of the above hypotheses.

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