Predicting Biomass from Snout–Vent Length in New World Frogs

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ABSTRACT.—In this study, we determined how well the snout–vent length (SVL) of anurans estimated their mass for 36 species in the New World. Linear regressions of log-mass on log-SVL were highly significant for all species, explaining more than 75% of the mass variation in most species, and over 50% of the mass variation in all species. We also investigated differences in the mass/SVL relationship within species, comparing juveniles to adults, females to gravid females, and males to females, to determine the importance of developing separate regressions for sex or life-stage classes. Three of six tests between juveniles and adults, and two of nine tests between females and gravid females, indicated statistically significant differences, although these differences had only minor effects on mass estimates. More statistical differences in regression equations occurred between males and females; again, these differences were unimportant for estimates of mass in some cases, but they were important where there was strong sexual size dimorphism within a species. Continued collection of both SVL and mass data in new field studies of anurans will provide broader analyses of mass/SVL regressions. These species regressions along with data on density can be used to determine anuran community biomass.

In moist, warm environments in temperate and tropical regions, anurans are a major component of ecosystems. Their roles in ecological pyramids are substantial (Whiles et al., 2006), although data on biomass generally are unavailable. Instead, anuran communities continue to be characterized by species richness and relative abundances. These variables are incorporated into classical ecological diversity indices, but alone, they do not encompass the dynamics portrayed by biomass and secondary productivity, which reveal the role that taxa or guilds play in ecosystem energy flow (Smith and Smith, 2001). Furthermore, local extinction of some species seems to be a global phenomenon, but how such declines affect anuran community biomass is essentially unexplored (Pounds, 2001; Collins and Storfer, 2003; Stuart et al., 2004; Lips et al., 2005).

Historically, anuran biomass may have been neglected in field studies, given the lack of accurate scales and balances at remote sites. However, snout–vent lengths (SVL) have been recorded from living individuals in the field or preserved ones in the laboratory, with little difference between measurements of living and preserved individuals (Lee, 1982). Consequently, there are extensive data sets of anuran SVLs, often without accompanying mass data. An exception is the anuran community at Cusco Amazónico, Peru (Duellman, 2005).

Herein, we explore the relationship between SVL and mass and its utility for estimating anuran biomass (excluding larval stages). Length-weight relationships have been useful in estimating biomass for a variety of organisms, including insects (Rogers et al., 1977; Schoener, 1980), spiders (Sage, 1982; Brady and Noske, 2006), sea turtles (Georges and Fossette, 2006), marine mammals (Trites and Pauly, 1998), and fish (Kohler et al., 1995; Martin-Smith, 1996; Froese and Palomares, 2000). In this study, we employ linear regression to determine how well SVL estimates mass for 36 species of frogs, and we discuss the implications of these regressions for estimates of community biomass. Because most anurans exhibit sexual dimorphism (Shine, 1979) and complex development with larval, juvenile, and adult stages (Duellman and Trueb, 1986), we also investigate differences in the mass/SVL relationships between sexes, between gravid and nongravid females, and between juveniles and adults.

MATERIALS AND METHODS

This study is based on data on anurans that we collected in the United States, Ecuador, and Peru. We included only species where SVL and mass were measured for at least 10 individuals.

In the United States, specimens were collected in Louisiana between August 2002 and September 2006, using a combination of opportunistic

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sampling and directed effort for particular species. For individuals captured and released on site, snout–vent length (to nearest 0.1 mm) was measured with dial calipers and mass (to nearest 0.01 g) with an electronic balance (Ohaus Scout Pro SP202). For these individuals, all frogs were captured and placed in zip-lock bags until all were measured. Frogs were only released once sampling of the site was complete. Collected specimens were taken live to Louisiana State University, anaesthetized in chloretone, and then measured with dial calipers (SVL to 0.1 mm) and weighed on an electronic balance (0.01 g; Sargent-Welch SWE-500). These specimens were fixed on a surface saturated with formalin and then draped with the same. All specimens were stored in 55% isopropanol or 70% ethanol at the Louisiana State University Museum of Natural Science (LSUMZ).

In Peru, specimens were collected at Cusco Amazónico, Departamento de Madre de Dios, discontinuously from January 1986 through December 1991. Mass (0.1 g) was measured in the field with pesola scales. Snout–vent length was measured (0.1 mm) with dial calipers between 1995 and 1997 on the preserved specimens. Similarly, specimens from Departamento de Loreto, Peru were collected in June and July 1993, weighed in the field, and SVL measured on preserved specimens in December 1993. All specimens were preserved in 10% formalin and stored in 70% ethanol at the University of Kansas Natural History Museum (KU).

In Ecuador, specimens were captured at Tiputini Biodiversity Station and Yasuní National Park, Provincia de Orellana, from April through May 2005, and from February through April 2006, using both randomly located litter plots and opportunistic sampling. Before being released on site, individuals were measured (SVL) in the field with dial calipers (0.1 mm) and weighed on an electronic balance (0.01 g; Ohaus Scout Pro SP202). As in Louisiana, individuals in a plot or given area were placed in zip-lock bags and not released until all frogs had been measured. Therefore, individuals were not sampled more than once.

Mass and SVL were log_{10}-transformed for least-squares linear regressions for each of the 36 species, following the equation: log-Mass = $log\ a + b$ log-SVL. From 1,492 specimens from the three countries, 15 were removed as outliers, based on studentized residuals (R Student). Generally, when the absolute value of an R Student observation is greater than 2, the observation is considered suspicious and its validity questionable (SAS Help and Documentation, SAS Institute, Inc., Cary, NC). To be conservative, we removed only observations

with an R Student larger than 4. We believe these extreme outliers to be a result of measurement or recording error.

Analyses of covariance were performed to test for differences in the mass/SVL (log/log) relationship between three sets of pairwise classes: juveniles versus adults, gravid females versus nongravid females, females versus males. Class (sex or stage) was used as a factor in the ANCOVA. We first tested for a difference in the SVL · class interaction which corresponds to the slope. If the slopes were not different, we then tested for a difference in class which corresponds to the intercept. When gravid females differed significantly from nongravid females, only the latter were compared to males; otherwise, all females were included in the female-male comparison. Only species for which more than five individuals were available in the data set for each sex or life stage were used in ANCOVA analyses.

For each species, we employed the significance level 0.05 to determine biological importance, reporting both the mass/SVL regression equation and its R^2- and P-values. However, for the ANCOVAs that compared the three subclasses within a species, we pursued one additional criterion to determine biological importance. When significant differences existed between juveniles and adults, the equation developed from all individuals (the ''species equation'') was used to predict mass for each individual. Then, the predicted mass for individuals of each stage, juvenile and adult, was compared separately to the actual mass of individuals of that stage in a paired t-test. This same method was applied to ANCOVA differences between gravid and nongravid females.

When females and males showed statistically different mass/SVL regressions through ANCOVA, we visually inspected the data with groups that may be sexually dimorphic, because males and females may not completely overlap in size (Hayek and Heyer, 2005). To determine biological importance of the separate sex regressions, we examined the overlap of the 95% confidence intervals of the regression equation for one sex with the data points for the opposite sex (i.e., did the data for the opposite sex fall inside or outside the 95% confidence limits?). All statistical tests were performed with SAS software (version 9.1.3, SAS Institute, Inc., Cary, NC).

The classification of anurans is in a state of flux. Herein, we follow the taxonomy of Hylidae proposed by Faivovich et al. (2005) and for Aromobatidae and Dendrobatidae proposed by Grant et al. (2006). However, for reasons given by Wiens (2007) and documentation given by Hedges et al. (2008), we recognize the family Eleutherodactylidae and do not

TABLE 1. Size ranges and linear regression coefficients for 36 New World frog species and for sexes separately in those species exhibiting important regression differences between males and females. All species regressions were significant ($P < 0.001$). All male and female regressions were significant ($P < 0.005$) with the exception of *Pristimantis fenestratus* males ($P = 0.21$).

| Species	Species ID	N	SVL (MM) Min.	SVL (MM) Max.	Mass (g) Min.	Mass (g) Max.	R^2	Slope	SE	Intercept
Bufonidae:										
Bufo fowleri	BuFo	13	43.40	73.80	7.42	39.24	0.99	3.01	0.10	−4.07
Bufo terrestris	BuTe	13	43.50	72.90	6.31	33.25	0.93	3.05	0.25	−4.14
Bufo nebulifer	BuNe	67	12.30	79.90	0.15	46.64	1.00	2.94	0.02	−4.00
Bufo "margaritifer" (Ecuador)	BuMaE	67	7.40	67.90	0.04	26.95	0.99	3.00	0.03	−4.04
Bufo "margaritifer" (Peru)	BuMaP	66	40.50	67.20	5.00	29.50	0.93	3.04	0.10	−4.13
Aromobatidae:										
Allobates trilineatus	CoTr	49	11.40	18.60	0.20	0.54	0.65	1.95	0.22	−2.76
Allobates femoralis	AlFe	28	8.50	26.60	0.09	1.85	0.94	2.64	0.12	−3.56
Dendrobatidae:										
Ramitomeya duellmani	DeDu	11	9.20	16.70	0.11	0.48	0.83	2.04	0.31	−2.90
Ameerega bilinguis	EpBi	56	10.50	22.60	0.12	1.15	0.89	2.82	0.13	−3.80
Hylidae:										
Acris crepitans	AcCr	75	11.10	27.70	0.15	1.69	0.95	2.87	0.08	−3.89
Dendropsophus leucophyllata	DeLe	42	28.30	40.20	1.10	7.50	0.76	4.17	0.37	−5.96
Nongravid females		11	32.70	40.20	1.90	7.50	0.72	4.68	0.89	−6.73
Males		31	28.30	35.30	1.10	2.60	0.28	2.31	0.70	−3.19
Hyla cinerea	HyCi	24	25.00	56.30	0.86	10.82	0.94	3.13	0.17	−4.47
Hyla squirella	HySq	36	22.00	35.10	0.57	2.88	0.89	2.99	0.18	−4.16
Hypsiboas fasciata	HyFa	45	33.90	51.20	2.00	6.80	0.88	2.75	0.16	−3.92
All females		10	42.40	51.20	4.00	6.80	0.65	2.33	0.61	−3.21
Males		35	33.90	40.30	2.00	3.20	0.24	1.40	0.43	−1.81
Osteocephalus taurinus	OsTa	36	48.60	93.90	5.10	50.00	0.86	2.97	0.20	−4.27
Phyllomedusa tomopterna	PhTo	32	41.50	62.30	3.30	9.80	0.76	2.26	0.23	−3.11
Phyllomedusa vaillanti	PhVa	52	20.30	76.20	0.30	35.50	0.95	3.06	0.10	−4.40
Scinax ictericus	ScIc	108	26.30	36.70	0.90	2.70	0.50	3.05	0.30	−4.32
Scinax pedromedinae	ScPe	71	20.30	31.50	0.50	2.20	0.81	2.70	0.16	−3.81
Eleutherodactylidae:										
Isodactylus nigrovittatus	ElNi	15	14.10	23.70	0.32	1.27	0.96	2.82	0.17	−3.74
Pristimantis fenestratus	ElFe	46	14.10	51.00	0.20	10.00	0.89	2.32	0.12	−2.99
Nongravid females		15	38.70	51.00	4.80	10.00	0.79	2.16	0.43	−2.69
Males		19	23.40	33.30	1.60	3.30	0.09	−0.60	0.39	1.28
Pristimantis ockendeni	ElOc	30	7.30	29.50	0.03	1.87	0.96	2.85	0.11	−3.92
Pristimantis peruvianus	ElPe	50	15.70	41.40	0.50	5.80	0.90	3.05	0.15	−4.19
Pristimantis toftae	ElTo	62	17.00	27.30	0.20	1.40	0.91	3.30	0.14	−4.56
All females		26	18.90	27.30	0.60	1.40	0.80	2.62	0.24	−3.62
Males		35	17.00	19.80	0.20	0.60	0.73	5.03	0.58	−6.76
Oreobates quixensis	IsQu	22	16.70	54.10	0.20	18.50	0.96	3.23	0.15	−4.42
Leptodactylidae:										
Adenomera hylaedactyla	AdHy	22	7.20	27.80	0.10	2.23	0.81	1.97	0.21	−2.72
Edalorhina perezi	EdPe	28	24.60	36.70	1.30	4.63	0.90	3.17	0.21	−4.27
Leptodactylus didymus	LeDi	46	17.30	58.60	0.40	16.50	0.98	2.88	0.07	−3.82
Leptodactylus rhodonotus	LeRh	26	62.90	83.10	21.00	55.00	0.62	2.40	0.39	−2.89
Physalaemus petersi	PhPe	36	15.50	37.40	0.30	5.44	0.87	2.90	0.20	−3.96
Microhylidae:										
Chiasmocleis bassleri	ChBa	15	16.80	29.90	0.50	3.87	0.85	2.83	0.33	−3.74
Elachistocleis ovalis	ElOv	25	30.00	43.80	2.70	5.60	0.59	1.48	0.26	−1.74
Gastrophryne carolinensis	GaCa	25	11.90	32.30	0.14	2.59	0.98	2.86	0.08	−3.89
Hamptophryne boliviana	HaBo	68	24.00	36.70	1.30	6.10	0.81	2.87	0.17	−3.77
Ranidae:										
Rana clamitans	RaCl	78	23.60	82.10	0.96	47.90	0.99	3.04	0.04	−4.14
Rana sphenocephala	RaSp	21	22.00	82.60	1.74	65.70	0.95	2.57	0.14	−3.31
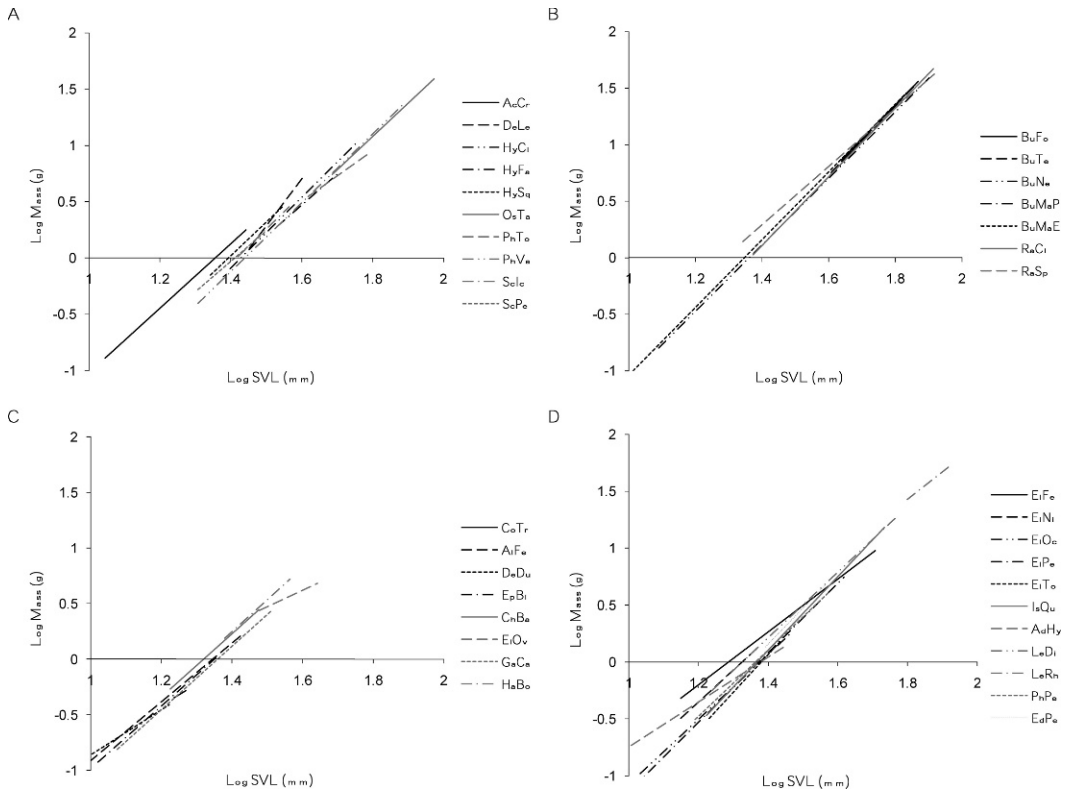
FIG. 1. Mass/SVL regression lines for (A) Hylidae; (B) Bufonidae and Ranidae, (C) Aromobatidae, Dendrobatidae, and Microhylidae; and (D) Eleutherodactylidae and Leptodactylidae. See Table 1 for species abbreviations.

follow the classification proposed by Frost at al. (2006).

RESULTS

We examined a total of 36 species of anurans belonging to seven families (Table 1). For each species, the linear regression of mass on SVL was highly significant ($P < 0.001$; Fig. 1A–D). Log SVL explained 75–100% of the variation in log mass for 32 of the 36 species (Table 1). In the other four species, SVL explained at least 50% of the variation in mass: *Allobates trilineatus* ($R^2 = 0.65$), *Scinax ictericus* ($R^2 = 0.50$), *Leptodactylus rhodonotus* ($R^2 = 0.62$), and *Elachistocleis ovalis* ($R^2 = 0.59$).

Sufficient data were available from six species for analysis of covariance between juveniles and adults in mass/SVL (Table 2). Statistically significant differences were detected in three species, with differing slopes between juveniles and adults in *Leptodactylus didymus* ($F_{1, 41} = 13.22$, $P = 0.001$) and differing intercepts in two species, *Ameerega bilinguis* ($F_{1, 53} = 10.01$, $P = 0.003$) and *Phyllomedusa vaillanti* ($F_{1, 49} = 11.86$, $P = 0.001$). However, in none of these three

cases (six tests, $P > 0.05$) was there a significant difference between the observed mass of one stage class and the mass predicted from the species regression equations.

Adequate sample sizes for nine species permitted ANCOVA tests of differences in the mass/SVL relationships between gravid and nongravid females (Table 2). Only two of the nine showed significant differences, one in the intercept, *L. didymus* (intercept $F_{1, 16} = 6.67$, $P = 0.020$), and one in the slope, *Phyllomedusa tomopterna* (slope $F_{1, 6} = 11.48$, $P = 0.015$). However, paired *t*-tests showed no differences (four tests, $P > 0.05$) between the observed mass of individuals of each group of females and the mass of individuals predicted from the species equation.

Sufficient sample sizes allowed comparison of mass/SVL regressions between females and males in 16 species (Table 2). Although eight of the 16 species exhibited statistically significant differences between males and females, four of these showed strong overlap of the 95% confidence intervals of the separate mass/SVL regressions for one sex and the points of the opposite sex (Fig. 2 A–B). The remaining four

TABLE 2. Results of ANCOVA tests for regression differences between sexes and age classes within species. Significant *P*-values are in bold. J = juveniles; A = adults; F = females; G = gravid females; M = males; F(G) = females and gravid females pooled. See Table 1 for Species ID.

Species	Comparison	N	Slope		Intercept	
			F	P	F	P
BuMaE	J VS A	37 / 28	0.01	0.909	0.12	0.735
ElFe	J VS A	8 / 38	1.04	0.315	0.16	0.689
EpBi	J VS A	13 / 43	0.77	0.383	10.01	**0.003**
IsQu	J VS A	9 / 13	0.71	0.411	0.03	0.866
LeDi	J VS A	15 / 31	13.22	**<0.001**		
PhVa	J VS A	9 / 43	0.07	0.795	11.86	**0.001**
CoTr	F VS G	13 / 8	1.72	0.207	0.71	0.411
ElOv	F VS G	12 / 6	2.15	0.165	0.00	0.984
ElPe	F VS G	6 / 7	3.62	0.090	0.75	0.406
ElTo	F VS G	16 / 10	1.81	0.192	0.19	0.663
HaBo	F VS G	24 / 10	0.01	0.927	1.75	0.196
HyFa	F VS G	5 / 5	2.09	0.198	1.46	0.266
LeDi	F VS G	10 / 9	0.00	0.947	6.67	**0.020**
PhTo	F VS G	5 / 5	11.48	**0.015**		
ScIc	F VS G	22 / 5	1.57	0.222	0.35	0.557
BuMaP	F VS M	17 / 49	2.54	0.116	0.00	0.980
BuNe	F VS M	12 / 23	0.17	0.686	0.33	0.571
CoTr	F(G) VS M	21 / 22	2.80	0.104	1.78	0.191
DeLe	F VS M	11 / 31	4.36	**0.044**		
ElFe	F VS M	15 / 19	22.24	**<0.001**		
ElPe	F(G) VS M	13 / 30	3.47	0.070	1.39	0.245
ElTo	F(G) VS M	26 / 36	14.71	**<0.001**		
HaBo	F(G) VS M	34 / 34	3.11	0.083	8.11	**0.006**
HyFa	F(G) VS M	10 / 32	1.56	0.219	10.58	**0.002**
HySq	F VS M	14 / 19	5.56	**0.025**		
LeDi	F VS M	10 / 12	0.01	0.936	0.02	0.882
LeRh	F VS M	11 / 13	3.40	0.080	0.00	0.959
OsTa	F VS M	12 / 19	0.36	0.552	2.65	0.115
PhPe	F VS M	15 / 13	0.05	0.834	1.32	0.262
ScIc	F(G) VS M	27 / 81	3.09	0.082	47.53	**<0.001**
ScPe	F VS M	28 / 39	0.31	0.579	4.51	**0.038**

species demonstrated notable sexual dimorphism with little to no overlap of regression confidence intervals (Fig. 2 C–D). These latter four species may, in fact, require separate equations to estimate male and female mass/SVL relationships; hence, regressions for each sex are presented separately as well as combined (Table 1). All separate sex regressions are significant with the exception of male *Pristimantis fenestratus* (Table 1).

DISCUSSION

Estimating biomass from linear dimensions has been a useful technique in fisheries science (Ricker, 1973), dietary studies (Beaver and Baldwin, 1975), and conservation management (Trites and Pauly, 1998; Braccini et al., 2006) across a variety of organisms. Overwhelmingly for the anurans studied here, SVL predicted mass for individual species, suggesting that SVL data from past or future herpetological studies, combined with mass/SVL regressions and

population densities, can functionally predict community biomass across geographic and temporal scales. Such data could document changes in community biomass as well as serve as a baseline for changes in individual taxa. For example, in cases where an individual species has disappeared or become rare, it is critical to know to what degree the entire community has changed in composition and biomass. With the ability to estimate community biomass, changes in each taxon can be compared to overall community changes and changes at any one site compared to baseline data at other sites— for example, tropical montane sites to tropical lowland sites. Such information might prove useful for determining the relative sensitivity of different taxa to disease and environmental changes. In fact, monitoring through time may be one component of an overall strategy to track amphibian decline.

However, estimates of community biomass will only be as accurate as the underlying mass/SVL relationships and relative species contribu-
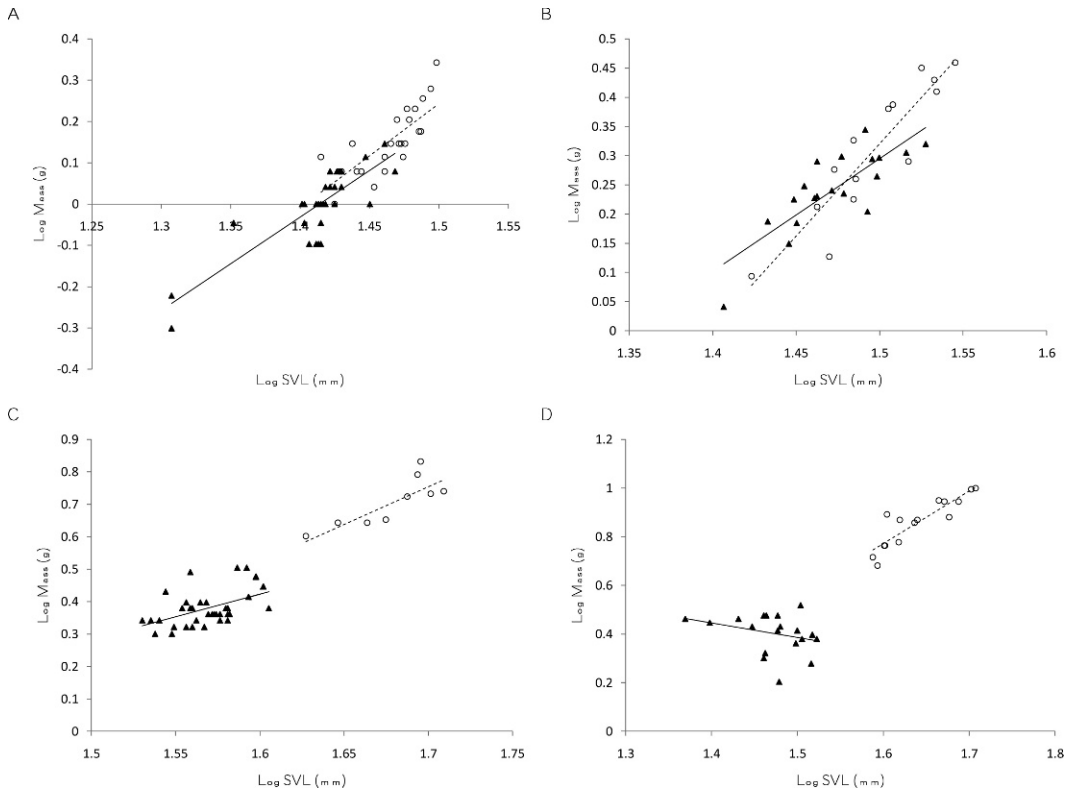
FIG. 2. Mass versus SVL plots showing differences in males and females of (A) *Scinax pedromedinae*, (B) *Hyla squirella*, (C) *Hypsiboas fasciatus*, and (D) *Pristimantis fenestratus*. Open circles represent females, and solid triangles represent males. Differences detected by ANCOVA for A and B are considered to be of little biological importance because of considerable overlap between sexes, whereas those detected for C and D are meaningful and show strong sexual dimorphism.

tions to the community. If the most abundant or largest species exhibit the worst mass/SVL regressions, the community biomass will be subject to error. In the four poorest regressions in this study, only 50–75% of mass was explained by SVL. Each of these four species is in a different family (Aromobatidae, Hylidae, Eleutherodactylidae, and Microhylidae); hence, there seems to be no taxonomic association with the poorer regression fits. Furthermore, these four species were represented by 26–108 individuals (Table 1), demonstrating no particular tendency toward rarity or abundance.

Likewise, different mass/SVL relationships for sex or size classes within a species could complicate community biomass estimates, particularly if sex/size dimorphisms occur in the more abundant or larger species in a community. Here, we concluded that only four cases showed biologically important differences within a species—*Dendropsophus leucophyllatus, Hypsiboas fasciatus, P. fenestratus*, and *Pristimantis toftae* (Table 1). All exhibit strong sexual size dimorphism (Duellman, 1978, 2005; Bartlett and

Bartlett, 2003). In cases in which such sexually dimorphic species dominate a community, separate mass/SVL regressions may be important in estimating community biomass. In the present study, we tested relationships using data already in hand. In the future, it would be prudent to pursue individuals of both sexes across the range of sizes during data collection.

Although we limited our study to species-specific relationships of frogs, further analyses with larger data sets and more species could compare relationships for higher taxa, such as genera and families. For example, a posteriori review of our data set (Table 1), suggests that the slopes of the log-log mass/SVL regressions appear to be more uniform within the Bufonidae (2.9–3.0) than within the Hylidae (2.3–4.2), a result that probably reflects the uniform body shape of bufonids relative to hylids (Fig. 1A–B; Duellman and Trueb, 1986).

Here, we were restrained in predicting mass/SVL relationships for higher taxa, given potential disparities in our data set, because of different researchers with different mensuration
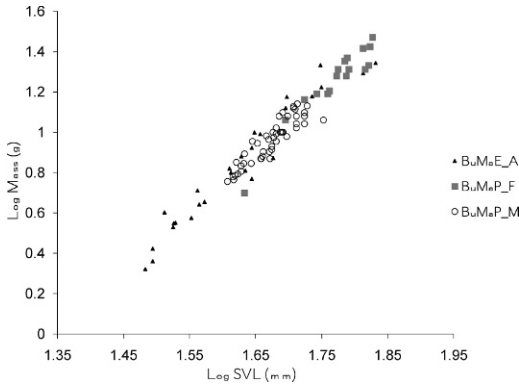
FIG. 3. Mass versus SVL plot of individuals of the *Bufo* ''*margaritifer*'' complex (BuMa), demonstrating variation between geographic regions (E = Ecuador, P = Peru) and sexes (A = adults of unknown sex, M = males, F = females). Regression lines for each group visually overlap at this scale; hence, they are not shown here.

tools. Still, the strength in the mass/SVL relationship overrode such variation in sampling protocol. For example, our *Bufo* ''*margaritifer*'' were collected either by JLD in Ecuador in 2005–06 and weighed on an electronic balance or by WED in Peru in 1986–91 and weighed with pesola scales. In addition, *B.* ''*margaritifer*'' apparently is a complex of several species across neighboring countries and perhaps within sites (Duellman and Mendelson, 1995; Cisneros-Heredia, 2006). Despite these opportunities for variation, our individuals of *B.* ''*margaritifer*'' exhibited a remarkably strong mass/SVL relationship (Table 1, Fig. 3), adding credence to the prospect of biomass analyses across different regions where data are contributed by different researchers.

To assure the accuracy of community biomass estimates, two steps are recommended. First, it is necessary to establish the mass/SVL relationships for many additional anuran species through field measurements on large numbers of individuals with care to include all sexes and sizes, moving toward more accurate mass measurements with electronic field balances rather than the traditional use of spring scales. Second, community studies that collect frogs according to standardized sampling protocols, such as litter plots or transects, should always include measurements of SVL and mass for undocumented species. Where such data are standardized, a user friendly database needs to be compiled, monitored, and made accessible to the scientific community.

Such a database could also incorporate prior studies where the amphibian community was sampled adequately with standardized meth-odologies. For example, litter plots have been employed across many tropical regions and often repeated through time at some sites (Scott, 1976; Inger, 1980; Allmon, 1991). Using modern mass/SVL relationships, community biomass could be determined for these older studies if SVL data were recorded for the individuals captured. For some sites, these historical data over 50 yr would span the entire recent history of amphibian decline (Whitfield et al., 2007).

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