Size-gradation in Syntopic Frogs in South India

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Abstract. -An assemblage of eight metamorphosed anuran amphibians were studied at a seasonal locality in South India to examine patterns of body size-gradation. In general, body shape was found to be closely correlated to ecological characteristics of the species. The mean ratio of linear dimensions of the body in adjacent species, when arranged in a size-series was 1.3 (range 0.83-1.88), as predicted by Hutchinson (1959) for closely-related sympatric species. It was concluded that competition may be at work in producing these ratios.

Key words: Amphibia, Anura, India, body size, competition.

Introduction

The body forms and sizes of organisms have been considered, since the time of Darwin (1859), to be determined by the powerful forces of natural selection, and may mirror a wide range of ecological interactions often too complex to comprehend in their entirety. The concept of a form-function relation appears to have stood the test of time, and is central to the problem of organismic evolution (Gans, 1988). Animal size, for example, may be an evolutionary response to demands of the immediate environment, related to key life history traits, such as fecundity, foraging, locomotion, and reduction of predation, desiccation, heating and cooling. Some workers (e.g. Hutchinson, 1959; Schoener, 1986a) have argued that smaller species are generally more specialized, as reflected in their restricted diets and geographical ranges. Gould (1966), however, considered both large and small species to be viable strategists, optimal size, according to Phillipson (1981) being dependent on competitive abilities and survival probabilities of the various size and age classes. However, large species tend to appear later in a group's evolutionary history, an exception being the Amphibia (Peters, 1983).

Within ecological communities, if environmental resources are partitioned according to dimension, as documented by Schoener (1965) and subsequent workers (reviewed by Schoener, 1974; 1986b), differences in the comparative sizes of the organisms are to be expected. In fact, such apparent differences were reported much earlier by Hutchinson (1959), who found constant differences in the ratios of linear dimensions of the trophic (feeding) apparatus among closely-related sympatric species in his now controversial "Homage to Santa Rosalia, or why are there so many kinds of animals?" paper. Hutchinson argued that similar species could coexist if the ratios of linear dimensions and weights of presumed competing species are around 1.3 and 2.0 respectively. While possible causal factors remain unclear, such ratios have been found in a wide range of both invertebrate and vertebrate communities, including beetles, spiders, frogs, lizards and birds (reviewed by Schoener, 1986a).

In this paper, I report patterns of body size and shape, and of size-gradation observed in metamorphosed anurans from a locality in South India. Specifically, I searched for patterns of size gradation within the eight syntopic frog species.

Materials and Methods

Eight species of anuran amphibians occur in sympatry in the coastal scrublands of Chengai Anna District, Tamil Nadu State, South India. These, along with their mean snout-vent lengths have been listed below:

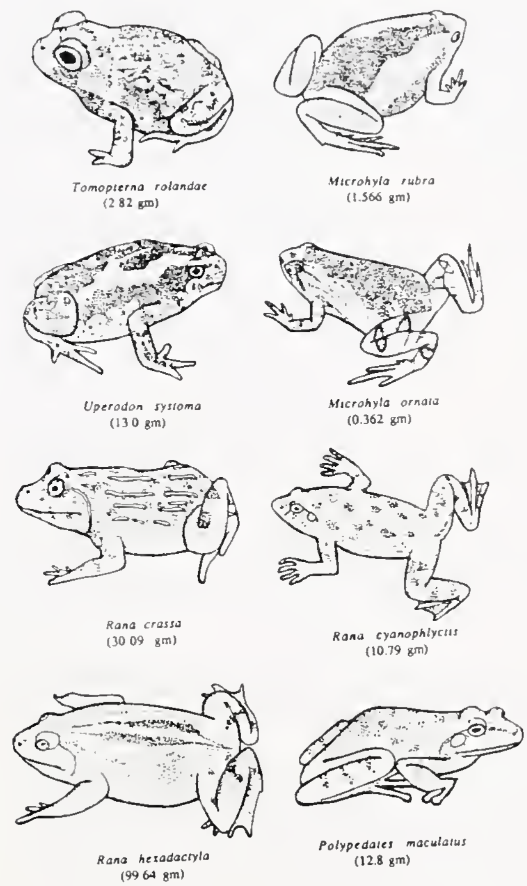

FIG. 1. Shapes and masses of the species studied. Figures in brackets are mean weights.

Microhyla ornata (4.1 mm), *M. rubra* (7.2 mm), *Tomopterna rolandae* (10.9 mm), *Uperodon systoma* (12.4 mm), *Polypedates maculatus* (20.9 mm), *Rana cyanophlyctis* (16.1 mm), *R. crassa* (22.9 mm) and *R. hexadactyla* (33.4 mm).

Abbreviations used include SVL (snout-vent length), HW (head width at the angle of the jaws, perhaps better defined as the gape), TBL (tibia length, the distance from the convex surface of knee to the convex surface of heel, with both tibia and tarsus flexed) and WT (wet body weight). Linear measurements were taken to the nearest 0.1 mm with a Mitutoyo Dial Vernier Caliper, weights were taken to the nearest 0.1 gm with an Acculab Electronic Balance (Model 333).

To interpret shape changes, logarithmic transformations of the dimensions of the organ of each species were used in the function $\log y = b \log x + \log a$ (where x and y are the morphological variates), which has been considered to approximate shape change in most organisms (see Gould, 1966, for justification).

Observations

The assemblage of eight anuran species studied display a range of body forms (Figure 1) and sizes (Table 1). Except for the diminutive species of the genus *Microhyla* (maximum SVL 17.4 and 26.5 mm) and the large ranid, *Rana hexadactyla* (maximum SVL 132.2 mm), all species were small to medium, with maximum SVL between 43.2 to 93.1 mm (mean 68.2).

A general impression is that some species are comparatively short and squat, while others are long and thin. To quantify differences, WT was divided by the cube of the SVL for individuals of each species. Three morphological groups along a continuum were recognized based on the patterns of body form (length-weight data in Table 2), which comprise species with similar ecological preferences, including heavy-bodied, terrestrial forms; light bodied aquatic forms; and an arboreal form of intermediate body mass.

The relationships of untransformed values of WT/SVL^3 (Figure 2.1), as well as the arcsine-transformed data (Figure 2.2) can be described as linear, the slope b being 0.38 and 1.89 respectively, not differing significantly (t-test, $P>0.05$) from isometry, indicating that large frogs are not likely to be comparatively lighter.

The ratios of differences in linear dimensions (SVL, HW, ED and TBL) and weight (WT) of frogs from this study, arranged in a size series (mean dimensions divided by corresponding figures for *Microhyla ornata*, the smallest member of the assemblage) are shown in Figure 3. The range of ratios of SVL (1.57-6.17) appear greater than shown by Neotropical *Anolis* lizards, 1.01-1.46 (Duellman, 1978), or

TABLE 1. Morphometric data on the eight species of anurams studied. References to species: MO, *Microhyla ornata;* MR, *Microhyla rubra;* TR, *Tomopterna rolandae;* US, *Uperodon systoma;* RC, *Rana cyanophlyctis;* PM, *Polypedates maculatus;* RCR, *Rana crassa;* RH, *Rana hexadactyla.* References to body parts: SVL, snout-vent length; HW, head width; TBL, tibia length; WT, weight. Linear dimensions in cm; wights in gm.

Species	SVL range ($\overline{x}$±SE) (N)	HW range ($\overline{x}$±SE) (N)	TBL range ($\overline{x}$±SE) (N)	WT range ($\overline{x}$±SE) (N)
MO	1.27-1.74 (1.48±0.098) (4)	0.37-0.50 (0.41±0.030) (4)	0.63-0.87 (0.75±0.052) (4)	0.2-0.6 (0.362-0.099) (4)
MR	1.68-2.65 (2.32±0.120) (8)	0.53-0.83 (0.723±0.033) (8)	0.95-1.27 (1.41±0.038) (8)	0.80-3.00 (1.566±0.276) (8)
TR	1.72-4.32 (2.70±0.100) (44)	0.76-1.88 (1.09±0.037) (44)	0.77-1.55 (0.99±0.034) (41)	0.50-9.09 (2.82±0.420) (33)
US	3.46-5.47 (4.38±0.320) (5)	1.05-1.49 (1.24±0.084) (5)	1.16-1.64 (1.40±0.139) (3)	3.00-20.00 (13.00±3.719) (4)
RC	2.40-7.07 (4.435±0.111) (74)	0.82-2.43 (1.61±0.331) (74)	1.16-3.42 (2.30±0.106) (32)	1.20-42.80 (10.79±0.940) (68)
PM	2.95-7.92 (5.97±0.510) (11)	1.05-2.72 (2.09±0.17) (11)	1.75-3.58 (2.80±0.235) (9)	1.40-28.00 (12.80±3.195) (10)
RCR	2.33-9.31 (6.32±0.233) (63)	0.85-3.36 (2.29±0.080) (63)	0.74-4.11 (2.33±0.190) (28)	1.00-77.77 (30.09±2.574) (62)
RH	1.51-13.22 (9.13±0.099) (461)	0.56-5.24 (3.34±0.040) (432)	0.62-5.66 (4.65±0.080) (164)	0.30-280.00 (99.64±2.454) (461)

Philippines scincid lizards, 1.41-4.33 (Auffenberg and Auffenberg, 1987). Ratios of HW (here considered the measure of the trophic apparatus) which may be more meaningful for understanding differences in morphology that may be the result of differences in feeding patterns, in the present study were somewhat greater than SVL ratios, the mean 4.3 (range 1.61-8.15). Mean values of the SVL, HW and WT ratios appear to be arranged in pairs that do not reflect phylogenetic affinities, and the implications, if any, are unclear. The incremental increase in SVL from the smallest to the largest species varied between 2.93-60.99, and no regular pattern of increment between adjacent species seems evident, although Auffenberg and Auffenberg (op. cit.) found that the greatest size differences exist among the smallest species in the skink community they studied.

TABLE 2. Weight to cube of snout-vent length in the eight species of anurans studied.

Species	range	($\bar{x}$±SE)	N
Microhyla ornata	0.047-0.115	(0.079±0.017)	4
Microhyla rubra	0.146-0.403	(0.221±0.033)	8
Uperodon systoma	0.289-1.297	(0.933±0.229)	4
Tomopterna rolandae	0.097-0.701	(0.295±0.030)	33
Polypedates maculatus	0.158-1.22	(0.646±0.127)	10
Rana cyanophlyctis	0.167-2.209	(0.745±0.049)	68
Rana crassa	0.079-2.903	(1.394±0.092)	62
Rana hexadactyla	0.064-7.147	(3.355±0.062)	461

Ratios of linear dimension of the body in adjacent species, when arranged in a size-series (Table 2) appear close to the Hutchinsonian ratio, mean values for all species ranging between 0.83-1.88 (mean 1.32± SE 0.09). Weight ratios were, however, 0.83-4.60, the mean 2.63 (±SE 0.56) substantially larger than 2.0 as predicted by Hutchinson.

Discussion

Morphologically similar species tend to display similar ecological need, and if they occur in sympatry, it is assumed that they compete.

Duellman (1978), in his study of the Ecuadorian herpetofaunal communities discovered no size groupings among frog and lizard species, using SVL ratios of differences between sympatric species, showing that there is, instead, a steady increase in SVL. Auffenberg and Auffenberg (1987) found that Philippines skinks show greater ratios of differences between species, and presumed predation on a significantly greater size range of prey by the scincids.

With *Microhyla ornata,* the smallest species in the area, was used as a standard against which all others were compared, the range of ratios of SVL (1.57-6.17) was found to be considerably greater than figures reported from other studies on tropical herpetological assemblages, including those of Duellman (1978) and Auffenberg and Auffenberg (1987), suggesting that members of the assemblage of South Indian amphibians under investigation feed on a greater size range of prey.

For coexisting frog species, the ratio of mean head width among species pairs appear close to the ratio for closely-related, sympatric and presumably competing species described by Hutchinson (1959) in studies from Canada (McAlpine and Dilworht, 1989) and Peru (Toft, 1980), indicating the potential for competition. The mean values (±SE) of the ratios of SVL, HW and WT for adjacent species in the South Indian amphibians were 1.31 (±0.09), 1.37 (±0.09) and 2.63 (±0.56), respectively.

The 1.3 ratio concept has recently come under close scrutiny, leading some workers (e.g. Strong et al., 1979; Simberloff and Boeklen, 1981) to doubt its constancy. In fact, Simberloff and Boecklen, op cit.) attempted to show that the methods utilized by workers reporting the constancy of the

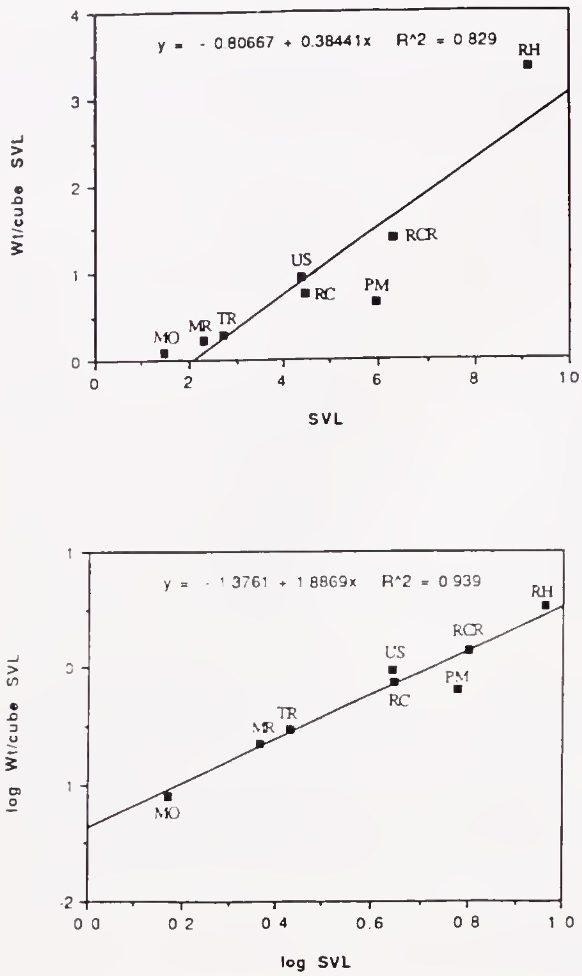

FIG. 2. Relationship between snout-vent length (SVL) and the ratio of weight to cube of snout-vent length (Wt/cube SVL) in the species studied. 2.1. Untransformed data; 2.2. Log-transformed data. Species abbreviations as in Table 1.

ratios have been erroneous, although subsequent workers have demonstrated that the evidence is, in many cases, quite strong on examination of fresh data (e.g. Schoener, 1984) or even on the basis of the tests conducted by Simberloff and Boecklen (see Losos et al., 1989). Maiorana (1978) suggested that if ecological segregation of two species (or age classes) requires a minimum level of overlap in their degree of morphological variability, the linear displacement in mean size will also be relatively constant, and argued that the presence of similar ratios in many man-made objects, as discovered by Horn and May

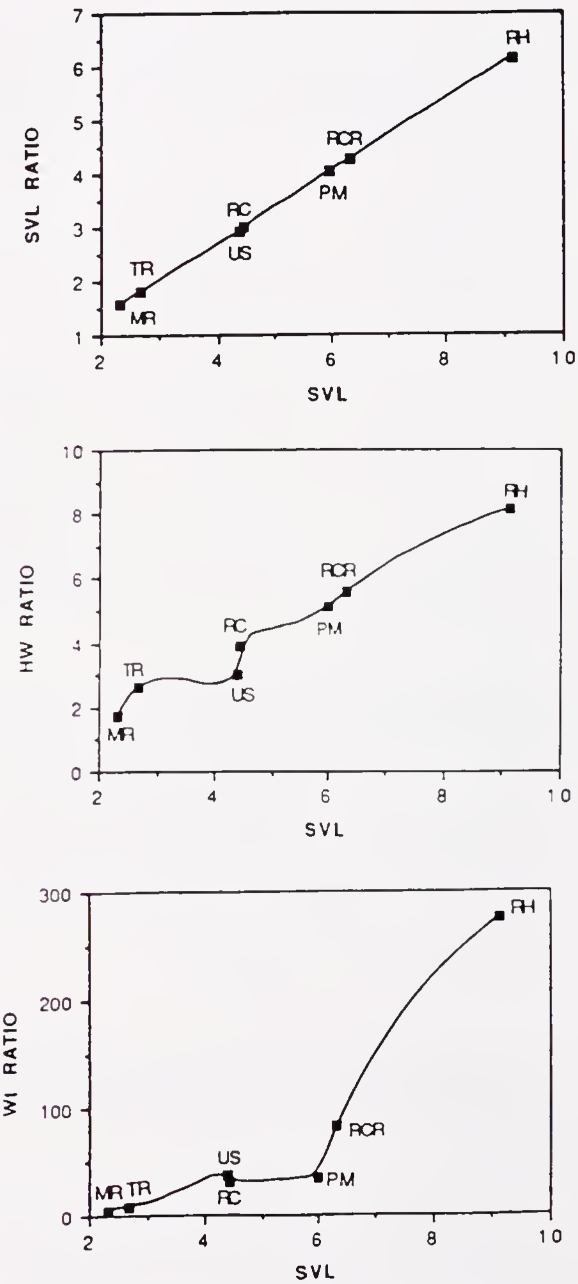

FIG. 3. Size-gradation in the species studied (mean dimensions divided by corresponding figures for the smallest species in the assemblage, *Microhyla ornata*. 3.1. Snout-vent length (SVL); 3.2. Head width (HW): 3.3 Weight (Wt).

(1977) may be associated with human perceptional abilities derived from the natural world.

The constancy of Hutchinsonian ratios has been shown for a large number of invertebrate and vertebrate groups (reviewed by Schoener, 1984; 1986a), which is suspected to be indicative of interspecific competition. To complicate matters further, ratios have been shown to be size-dependent, a function of allometry, and may thus change with growth (Roth, 1981). These are also thought to vary geographically, assemblages in the tropics show smaller ratios than temperate ones (Klopfer and MacArthur, 1961), suggestive of greater niche overlap in tropical assemblages. In the present study, HW, considered a measure of the trophic apparatus of frogs, showed negative ontogenetic allometry, the slopes b of the regressions of SVL and HW (on log paper) scaling allometrically in all eight anuran species that comprise the assemblage under investigation, indicating differences in the relative size and shape of the trophic apparatus among the different size-classes and sexes within a species may be influenced by food size.

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