

Anuran Locomotion—Structure and
Function, 2: Jumping Performance
of Semiaquatic, Terrestrial, and
Arboreal Frogs

GEORGE R. ZUG

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ABSTRACT

Zug, George R. Anuran Locomotion—Structure and Function, 2: Jumping Performance of Semiaquatic, Terrestrial, and Arboreal Frogs. *Smithsonian Contribution to Zoology*, number 276, 31 pages, 9 figures, 15 tables, 1978.—Frogs evolved as jumping machines. The earliest recognized anuran fossil possessed a foreshortened body and elongated hindlimbs, primary adaptations for jumping. The majority of extant frogs retain jumping as their primary mode of locomotion. Eighty species of frogs were tested to determine their absolute and relative (jumping distance divided by snout-vent length) jumping abilities. The species include representatives from the Ascaphidae, Bufonidae, Dendrobatidae, Pelodyadidae, Discoglossidae, Hylidae, Leptodactylidae, Microhylidae, Myobatrachidae, Pelobatidae, and Ranidae. Jumping performance is examined relative to taxonomic and habitat group, fatigue, body size, and sex. The ranking of jumping ability (distance jumped divided by body length) among the sampled species from weakest to strongest is Bufonidae, Pelobatidae, Discoglossidae, Microhylidae, Ranidae, Leptodactylidae, Dendrobatidae, Ascaphidae, Myobatrachidae, Hylidae, and Pelodyadidae for the families of frogs and semifossorial terrestrial, treetop arboreal, semiaquatic-terrestrial, terrestrial, scrub arboreal, and grass arboreal for the habitat groupings. Weak jumping species show little evidence of fatigue, whereas strong jumpers show a progressive decline in performance. Males tend to jump farther than equivalent-sized females, although the opposite or neutral situation occurs in a few species. Both inter- and intraspecifically, large frogs jump farther than small ones; however, a comparison of relative ability shows small frogs to be the strongest jumpers.

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Contents

	<i>Page</i>
Introduction	1
Acknowledgments	1
Historical Perspective	2
Jumping Tests	3
Jumping Performance	4
Intraspecific Variation	4
Body Size	6
Sex	10
Fatigue	14
Habitat	16
Taxonomy	18
Summary	21
Appendix: Basic Data	22
Literature Cited	30

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Introduction

Over two thousand species of frogs exist today. Their diversity spans the gamut from completely aquatic to completely arboreal, from ten millimeter to twenty-five centimeter bodies, and from oviparous to viviparous. In spite of this great diversity in habits and size, all frogs look much the same; a stout body joined directly to the head with no neck, no tail, and two pairs of well-developed limbs, the hind pair particularly enlarged. This body form reflects their evolution as jumping organisms. It is stamped upon all individuals and species, whether or not they retain jumping as their primary mode of locomotion.

While the majority of frogs are still jumpers, their jumping abilities are not equal. We recognize this in our everyday language by saying toads hop and frogs jump. Both verbs describe the simultaneous extension of the hindlimbs, which propels the animal forward suddenly, but recognize the difference in force applied or distance traveled. Just how variable is an individual's jumping performance: within a series of jumps, between conspecifics, and between species? What are the causes and the sig-

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nificance of this variation? This pair of general questions contain many subsets of questions. The purpose of this report is to determine the relationships of jumping performance to body size, sex, habitat preference, and taxonomy. Special attention is paid to the kinds of variations in jumping ability and the role of fatigue in jumping performance.

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Historical Perspective

If I were to have searched deep enough, I might have discovered that Aristotle or some Renaissance scholar was the first to investigate and describe the jumping ability of frogs. Unquestionably, Samuel Clemens, alias Mark Twain, was the first author (1865) to bring the weighty problem of frog locomotion to the attention of a large audience in his short story "The Celebrated Jumping Frog of Calaveras County." I might also note that Twain's classic work remains more readable than subsequent writers on the subject.

Versluys (1929) observed that the best jumping frogs are those with well-developed chalk sacs (= calcareous deposits in the endolymphatic sacs). In 1931, Hirsch published an extensive analysis of the mechanics of the jump of the frogs *Rana ridibunda*. Using cinematic and osteometric analysis, he examined the kinematics of the hindlimb and pelvic girdle segments from the initiation of a jump until take-off. He did not mention jumping distances or the possible modifications of the form or the speed of limb segment movements with different jumping performances. Wermel (1934) studied the relationship of body proportions (limb segment lengths to body length and particularly fore- to hindlimb length, i.e., heterotypy) on the jumping ability of 10 species of frogs, *Bombina bombina*, *B. orientalis*, *Pelobates fuscus*, *Bufo bufo*, *B. viridis*, *Hyla arborea*, *Rana arvalis*, *R. esculenta*, *R. ridibunda*, and *R. temporaria*. He determined jumping distance by averaging 50 jumps per individual and then established an index of relative jumping ability by dividing distance by body length. His values for jumping ability range from 1.7 for the weakest jumper to 7.2 for the strongest and a positive correlation between jumping ability and hindlimb length and a negative correlation between ability

and heterotypy. The investigations of both Hirsch and Wermel are models of thoroughness and provide the foundations and direction for future research.

Their studies, however, escaped the attention of or failed to interest researchers, and the study of frog jumping behavior lapsed into a period of anecdotal reports, such as Rose's (1950:17) report on the jumping prowess of South African frogs. There was a slight arousal of interest in the early 50's, when Rand (1952) described the jumping ability and endurance of six species of North American frogs, *Bufo fowleri*, *Acris crepitans*, *Hyla crucifer*, *Rana catesbeiana*, *R. clamitans*, and *R. pipiens*. He provided absolute jumping distances and relative jumping ability for these species and concluded that: (1) the jumping surface affects the length of the jump; (2) hindlimb length and habitat preference, but not body size, are correlated with jumping ability. Stokely and Berberian (1953) compared *Rana pipiens* and *R. utricularia* and found significant differences in the proportions of various hindlimb segments but no difference in jumping ability. The low values of their mean jumping distances suggest the jumps were abnormal, so their conclusions are probably invalid. Gray (1953) in his popular book on animal locomotion used the frog as an example to explain the physics of jumping. He discussed these principles briefly again in 1968. Gans (1961), in a similar vein, wrote a popularized account of frog jumping stressing the anatomy and kinematics of the hindlimbs as well as the physics of jumping. Davidson (1963) and Cox (1966) also published popularized accounts, a photo story, and general anatomy, respectively.

The actual jumping distances of the marine toad, *Bufo marinus*, were presented by Rand and Rand (1966). They showed that jumping distance and hindlimb length have a positive linear relationship. In a parallel note, Gans and Rosenberg (1966) modified a ballistic equation to show the relation between the force of the toad's jump and its weight.

In 1972, I published an analysis of the relationships between the relative jumping ability and proportions of the postcranial skeleton in four species of frogs, *Bufo marinus*, *B. terrestris*, *Hyla crucifer*, and *Rana clamitans* and showed that several of the fore- and hindlimb proportions are good indicators of jumping ability. Dobrowolska (1973) reported on a similar study for ten species of European frogs,

Bombina bombina, *B. variegata*, *Bufo bufo*, *B. calamita*, *B. viridis*, *Hyla arborea*, *Rana arvalis*, *R. esculenta*, *R. ridibunda*, and *R. temporaria*. She showed that hindlimb length is a good indicator of jumping ability and limb heterotopy a poor indicator. Gambaryan (1972) briefly mentioned the mechanics of frog jumping in a discussion of mammalian jumping gaits. Calow and Alexander (1973) analyzed muscles tension and size, joint movement, and force application during jumping in the frog, *Rana temporaria*. From their analysis, they developed a hypothesis on the operation of vertebrate muscles accelerating a mass from rest over a given distance. Claussen (1974) examined the influence of desiccation and bladder water reserve on jumping ability in *Bufo americanus*, *B. cognatus*, and *R. clamitans* and concluded that anurans in a physiologically unbalanced state do not jump as strongly as when physiologically normal.

Jumping Tests

All frogs were tested in rectangular jumping arenas or tracks in the laboratory. Although the basic arena and techniques were described earlier (Zug, 1972), it is necessary to repeat and expand upon this earlier description, because changing circumstances resulted in modifications to accommodate the different species of frogs and the available physical facilities. The North American, Caribbean, and European species were tested in a $1\frac{1}{2} \times 6$ m open-ended track with 1 m high walls extending parallel to the long axis. Since this arena was in the Division of Reptiles and Amphibians, temperature was fairly constant, 22° – 24° C. The Panamanian dendrobatids were tested in a basement corridor of the Balboa laboratory of the Smithsonian Tropical Research Institute; the track was approximately 2×3 m. Frogs were tested only in the morning, and the temperature range was 26° – 29° C. The New Guinean frogs were tested in a $1\frac{1}{4} \times 5$ m track, enclosed along the two sides and end by $1\frac{1}{4}$ m walls. The arena was in a storage barn, and the temperature range was 25° – 34° C with most trials performed between 28° – 31° C. The New Guinean frogs were tested in the morning, usually before 11:00 AM and occasionally in the late afternoon. Nonetheless, when testing a large series (15–20 individuals) of a single species, the temperature differential would be 2° – 3° C from the

first to the last individual tested. Testing of montane species, particularly the smaller ones, was restricted to periods when the temperature was 29° C or less. The temperatures at all three sites were recorded within the jumping arena, 5–10 cm above the floor.

The floors of all arenas were concrete or concrete and asbestos tile, covered with two or more layers of brown wrapping paper. This surface offers sufficient friction and resilience so that the jumping behavior and performance is equivalent to frogs jumping on a natural substrate (see discussion in Zug, 1972:617). If slipping occurred, it was usually on the first jump after release when posture tended to be abnormal and initial slipping jumps were not recorded.

The standard method used for the jumping tests was to blot the frog's venter (posterior abdomen and thighs) in nontoxic ink, set the frog down on the paper at one end of the arena, and have the frog jump five or more times. The frog was then caught and placed in a container with a small amount of standing water, just enough to immerse the frog's venter. The frog would rest in this for two or three minutes while the distances between the ink blotches of five consecutive jumps were measured and recorded. This sequence would be repeated for a second trial of five consecutive jumps. Upon completion of the second trial, each frog was anesthetized in a chlorotone solution, uniquely tagged, weighed, and measured, i.e., snout-vent length. Frogs were sexed by examination of the gonads.

Initially, I planned to obtain five trials of five jumps each for each individual. After testing nearly 200 frogs of 18 species, it became apparent that this scheme was too time consuming for the amount of information obtained. Furthermore, the jumping performance, at least of the small species, appeared to decline in successive trials in spite of the rest period between trials. Subsequent tests included only two trials of five jumps each. The tests were modified further for most of the Panamanian and New Guinean jumping experiments. The jumping performance of the second trial did not seem equivalent to the first, perhaps owing to the increasing temperatures during the tests, so the frogs (if willing) were jumped ten or more times in succession. This modification, by reducing the handling and stress of the frogs, produced a less variable measure

of performance, although the estimate of jumping ability was usually based on a sequence of seven or eight successive jumps rather than ten.

Handling and/or contact of the frogs was kept at a minimum before and during the test. Prior to testing, the frogs were touched only upon capture and upon transfer to a storage container in the laboratory. During testing, the frog was caught, blotted on ink, immediately released at one end of the test arena, caught and returned to a resting container at the end of the jumping trial. Most frogs were stimulated to jump by a sudden hand movement near them, although a few required a prod with a blunt probe. All individuals were wild caught and transported to the laboratory. With few exceptions, all frogs were tested within a week of capture, most within 48 hours of capture. The frogs were held in sealed containers (inflated plastic bags) with moist paper towels; the towels were replaced and the containers were rinsed with water daily.

The species tested are listed in Table A of the appendix. A listing of their jumping performances is in Table B (absolute jumping distances) and Table C (relative jumping abilities) and the body length-weight relationships in Table D of the appendix. The absolute jumping distance is reported as the sample average for the mean and maximum values of the actual distances jumped by each individual in the sample. The relative jumping ability is the mean and maximum jumping distances divided by the snout-vent length of the jumping individual. The mean and maximum relative jumping abilities of the species are averages of the means and maximums determined for individuals. Other parameters, particularly body weight, could have been used to obtain an estimate of relative ability; I chose to use body length here because it has been the standard measure since 1934. The other parameters will be analyzed later.

Jumping Performance

An attempt was made to include individuals of both sexes and a variety of age or size classes in each specific sample, in order to enhance the analytical potential of the samples. Samples with this diversity are, however, in the minority. Most frog species are cryptozoic and exposed to predation by herpetologists only during their breeding season, thus

many of the samples are composed largely of sexually mature males (see the third column in Table A of the appendix).

INTRASPECIFIC VARIATION.—The intraspecific variation in jumping performance—both absolute and relative—is high (see standard deviations and ranges in Tables B and C). A portion of this high variability may be due to the wide range of body sizes and the inclusion of both sexes in the species samples. Increased variability due to a wide range of body sizes within a sample is best demonstrated by a comparison of the standard deviation of the mean jumping distances (Table B) in similar sized species pairs with samples encompassing different size ranges. For example, *Bufo marinus* from Florida (snout-vent length range of sample, 72–116 mm) has a standard deviation of 53.9 mm and *B. marinus* from Papua New Guinea (14–172 mm) 107.4 mm; *Hyla squirella* (27–38 mm) 56.9 mm and *H. cinerea* (29–51 mm) 79.5 mm; or *Rana virgatipes* (34–55 mm) 49.3 mm and *R. clamitans* (31–88 mm) 159.2. In each pair, the sample with the smaller range has the lower variability, however, this trend does not always hold (e.g., *Bufo punctatus* and *B. terrestris*, *Hyla crucifer* and *H. squirella*, or *Rana clamitans* and *R. sylvatica*; first member of each pair has larger size range, yet lower variability). Even though body size is affecting intraspecific variation, it is only one component of variability and perhaps a minor one relative to the motivational and physiological state of the individual frog.

The maximum distance jumped by a frog is fixed by the biomechanical limits resulting from the structural organization of its locomotor apparatus. A frog probably attains its absolute maximum distance rarely, approaching the maximum when hard pressed by a predator attack. At other times, a frog adjusts the strength of its jumping kick to the circumstances: a long jump if frightened, a short one if changing resting location; long if healthy or well-fed, short if sick or starving; and other such comparative pairs. The point I wish to emphasize is that each frog controls its jump: how far it will jump as well as whether it will jump to the right or left, whether it will land facing toward or away from the disturbance. The control an individual has over its jumping performance was apparent throughout the test but is difficult to quantify other than by showing the variation in an individual's jumps or by anecdotal notes.

While I wish to emphasize an individual's control over its jumping performance, I do not wish to imply that its normal jumping performance will not be centered around an "optimum" distance that is species specific. This assumption on species specificity has been proven valid in previous investigations, e.g., Rand (1952) and Dobrowolska (1973), and as illustrated in Tables B and C. Different species jump different distances no matter how the species are tested or reported. Furthermore, different species may in the wild use different jumping patterns, i.e., a fixed sequence of alternating long and short jumps and directional changes (e.g., Gans, 1960:304). Testing and analysis may, however, alter the jumping performance results of different researchers. Jumping performance is usually reported as an average of the actual distances jumped and/or as a relative distance (average jumping distance divided by snout-vent length). Wermel's (1934) and Dobrowolska's (1973) data (Table 1) are quite sim-

ilar in spite of different testing methods. Wermel's frogs jumped 50 times each. Dobrowolska's 10 times each; the jumps were consecutive in the latter and presumably so in the former. I would have expected Dobrowolska's data to be higher in the strong jumpers (*Hyla* and *Rana*), since fatigue or possibly repeated handling might cause a reduction in jumping distance during a sequence of 50 jumps.

There is less similarity between my data and Rand's (Table 2), than in the previous comparison. This dissimilarity is in part due to differences in testing and analysis. While both of us used the mean of 10 jumps for the absolute distance, Rand usually had five or fewer individuals so individuals were often tested two or three times. His tests were typically performed outdoors on natural substrates, apparently immediately following capture. His relative distance was determined by dividing the maximum rather than the mean jumping distance by body length, resulting in higher values. In absolute

TABLE 1.—A comparison of the mean jumping data of adult European frogs from Wermel (1934) and Dobrowolska (1973) (relative distance value of Dobrowolska were read from her bar graphs and may be in error by ± 0.1)

Taxon	Sample size		Absolute distance (mm)		Relative distance (%)	
	W	D	W	D	W	D
<i>Bufo bufo</i>	5	17	123	116	1.9	1.5
<i>Bufo viridis</i>	10	21	154	157	2.8	2.5
<i>Bombina bombina</i>	10	27	138	155	3.2	3.8
<i>Hyla arborea</i>	10	30	273	406	7.5	9.8
<i>Rana arvalis</i>	5	21	329	390	7.0	6.6
<i>Rana esculenta</i>	7	21	324	371	5.4	5.6

TABLE 2.—A comparison of the mean jumping data of North American frogs from Rand (1952) and Zug (Tables B and C, "Appendix") (see text for discussion of difference in testing and analysis)

Taxon	Sample size		Absolute distance (mm)		Relative distance (%)	
	R	Z	R	Z	R	Z
<i>Bufo fowleri</i>	10	25	453.5	248.9	7.8	5.2
<i>Acris crepitans</i>	10	24	701.6	429.4	36.2	21.9
<i>Hyla crucifer</i>	10	36	296.3	504.9	17.9	19.1
<i>Rana catesbeiana</i>	10	20	542.8	708.0	8.9	7.7
<i>Rana clamitans</i>	10	37	665.8	613.7	11.5	10.8
<i>Rana pipiens complex</i>	10	24	785.0	714.8	12.9	12.2

distance, Rand's *Bufo* and *Acris* data are significantly higher than mine (Student $t = 6.65$ and 7.13 , $df = 31$ and 32 , respectively), whereas my *Hyla* and *R. catesbeiana* data exceed his. For *B. fowleri*, Rand's sample included only adults, whereas mine included predominantly subadults and juveniles; he also obtained a mean of 261 mm when he tested the toads on sand rather than grass. There is no satisfactory explanation for differences of our *Acris* samples, other than most of the individuals in my sample were tested 7 or 8 days following collection. Casual observations of other samples suggest that jumping performance is inversely related to length of time in captivity; however, I am doubtful whether a difference of nearly 300 mm can be attributed to captivity time alone. Similarly, there is no clear explanation for the differences in our *H. crucifer* and *R. catesbeiana* data. Rand did note a reluctance for the *crucifer* to jump voluntarily after the first several jumps, yet the maximum jump of only one of his samples exceeds the means of my data.

High variation is not unexpected in a complex behavioral trait, such as locomotion, which must constantly be adjusted to meet the needs of an individual. Perhaps we should be surprised that it is not more variable. Although there is a tendency for the long or strong jumpers to exhibit greater variability in jumping distances (most apparent in the comparison of relative jumping ability, Table C), this trend has exceptions. For example, *Ascaphus* and *Sphenophryne* have a jumping ability two to four times greater than *Bufo*, yet all three taxa share a similar level of variation. Obviously many parameters influence variation in jumping performance; the following sections examine a few of them.

BODY SIZE.—Those species (Table 3) with a wide range of body lengths form the subset for comparison. Examination of Table 3 and Figure 1 show that only those samples encompassing the entire size range from postmetamorphosis to adult possess a significant and strong correlation, i.e., linear correlation coefficient greater than 0.80, between body length and jumping performance. *Sphenophryne palmipes* is the only exception in this group containing also *Bufo marinus* (from Papua New Guinea), *Eleutherodactylus antillensis*, *E. lentus*, *Litoria infrafrenata*, *Rana clamitans*, and *R. grisea*, and it contains mid-juvenile to adults. Eleven other species have significant linear correlation coefficients.

These eleven species (*B. americanus*, *B. fowleri*, *B. marinus* (from Florida), *B. terrestris*, *Dendrobates auratus*, *Acris crepitans*, *A. gryllus*, *Hyla cinerea*, *H. versicolor*, *Platymantis papuensis*, and *Rana catesbeiana*) and *Scaphiopus couchi*, which have a correlation coefficient greater than 0.50, also demonstrate a correlation between body length and jumping ability; however, the correlation is not as strong. While correlation coefficients (r) of 0.50 or even lower may be statistically significant, I consider only those regressions with $r \geq 0.80$ as biologically significant, since r^2 (coefficient of determination) roughly describes the amount of variance or scatter accounted for by the regression equation and its curve. Thus regressions with $r \geq 0.80$ account for two-thirds or more of the variance, whereas for example, the regression line accounts for only 30% of the variance in *americanus* or 55% in *R. catesbeiana*. The correlation coefficients of the seven remaining species are too low to demonstrate an association between length and jumping distance. Nonetheless with the majority of the species (Figure 2) showing a positive relation between jumping distance and body length, this correlation probably exists for most anuran species. The absence of this correlation in some of my samples is due primarily to restricted size classes in these samples and secondarily from high variability in the performance of individuals within the samples. Body length was also compared to maximum jumping distance for eleven species (Table 3), and the correlation in this subsample is no better or worse than for the entire sample of 26 species.

The preceding discussion was based on an interspecific comparison of the linear regression equations. The data were analyzed by the Hewlett-Packard family regression program (H-P Model 10 Plotter Stat Pac, Vol. 1), which also provided exponential, parabolic, and power equations and their correlation coefficients. In most cases, the correlation coefficients of the latter three equations were similar to that of the linear equation. This similarity can be seen by comparing the linear and power correlation coefficients in Table 3. I consider linear or power equations best to describe the trend of the points, because a visual examination of the linear and power curves appears to include all clusters of points. Furthermore, I find it difficult to accept the exponential explanation, which requires that jumping ability becomes progressively

TABLE 3.—The effect of size (snout-vent length, X, mm) on jumping performance (mean jumping distance, Y, mm) in 26 species of frogs as shown by linear and power regression equations (A = y-axis intercept, B = slope, r = correlation coefficient, max = maximum jumping distance, * = probability significance of 0.05 or smaller; sample size and snout-vent length range are in Table A of the appendix)

Taxon	Linear (Y=A+BX)			Power (Y=AX ^B)		
	A	B	r	A	B	r
A. truei.....	98.32	12.00	.88*	25.26	0.85	.89*
B. americanus.....	84.21	2.23	.55*	23.74	0.54	.55*
max.....	74.31	3.24	.66*	18.34	0.65	.68*
B. fowleri.....	64.12	3.89	.55*	17.22	0.68	.52*
B. marinus (FL).....	184.11	2.34	.60*	32.50	0.55	.59*
B. marinus (PNG).....	103.46	2.46	.89*	16.99	0.66	.95*
max.....	122.71	3.17	.87*	18.24	0.70	.94*
B. terrestris.....	131.88	1.63	.46*	38.40	0.44	.55*
C. inguinalis.....	211.83	5.30	.33	88.69	0.42	.40
D. auratus.....	13.32	5.93	.74*	5.75	1.03	.76*
max.....	109.06	5.29	.50*	27.71	0.67	.55*
A. crepitans.....	-60.96	25.07	.75*	14.96	1.12	.69*
A. gryllus.....	-85.84	27.78	.45*	6.98	1.39	.60*
max.....	116.36	25.33	.35*	29.97	1.00	.48*
H. cinerea.....	257.70	6.23	.56*	76.14	0.51	.59*
H. versicolor.....	29.48	9.96	.46*	7.49	1.09	.50*
O. septentrionalis.....	514.73	4.78	.39*	143.45	0.42	.42*
max.....	604.42	4.99	.37	173.45	0.40	.41*
E. antillensis.....	17.06	9.66	.81*	23.71	0.73	.68*
E. lentus.....	2.98	15.07	.84*	25.50	0.83	.82*
E. martinicensis.....	212.84	1.05	.10	129.77	0.18	.17
max.....	229.15	2.20	.17	107.70	0.29	.24
C. cryptotympanum.....	368.53	0.56	.05	290.90	0.28	.05
G. carolinensis.....	131.54	2.21	.14	81.47	0.25	.14
max.....	224.75	-0.01	-.05	234.14	-0.02	-.05
S. palmipes.....	68.07	11.98	.89*	21.12	0.88	.91*
S. couchi.....	141.83	1.57	.57	46.62	0.40	.62*
max.....	222.35	0.69	.20	126.15	0.18	.24
S. holbrookii.....	161.61	0.69	.41	97.17	0.18	.54
L. impura.....	783.56	5.66	.22	381.28	0.26	.24
L. infrafrenatus.....	80.65	12.30	.92*	6.96	1.16	.94*
max.....	78.71	14.16	.92*	7.80	1.16	.94*
P. papuensis.....	342.81	11.18	.53*	67.57	0.66	.57*
max.....	505.41	9.52	.47*	144.29	0.49	.51*
R. catesbeiana.....	359.33	3.41	.74*	71.68	0.50	.79*
R. clamitans.....	142.81	8.07	.87*	32.96	0.72	.87*
max.....	178.39	9.39	.86*	37.57	0.73	.87*
R. grisea.....	168.02	13.75	.93*	26.85	0.88	.96*

better with increasing body length, or the parabolic explanation, which theoretically requires a plateau of performance with equivalent increasing or decreasing performance on each side of the plateau.

It is clear from the above data that jumping ability within a species is directly related to body length, Wermel (1934) was the first to comment on this trend and noted that in *Rana temporaria* jumping distance increases 4.39 cm for each additional cm increase in body length. Comparable

values are found in the linear slope (B) column of Table 3. Rand and Rand (1966) demonstrated a positive linear relationship between hindlimb length and jumping distance in *Bufo marinus*, roughly B = 2, which matches the slope of my samples of *Bufo*.

By using relative jumping ability, the size factor can be removed from the actual jumping distance, in order to determine whether different size classes show different jumping abilities. When Wermel (1934) examined *Rana temporaria* in this way, he

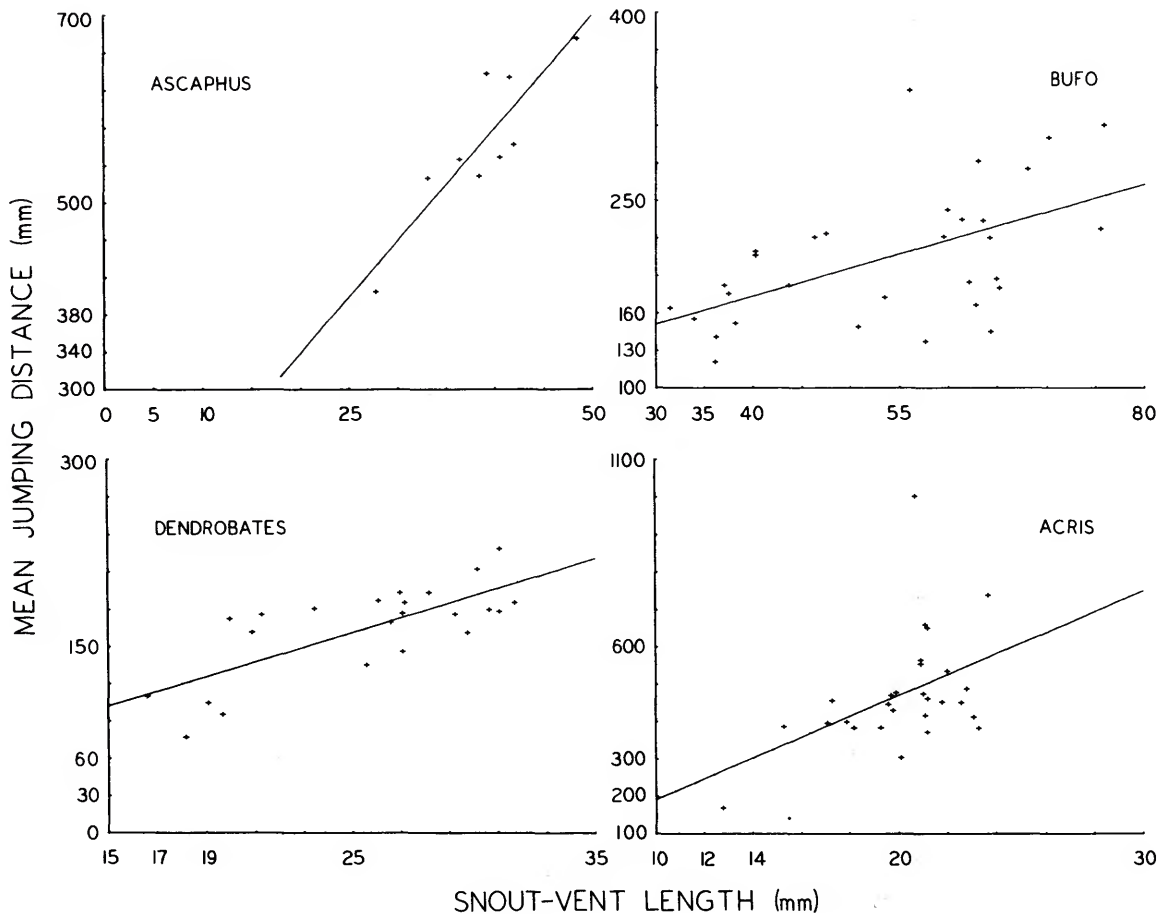


FIGURE 1.—Examples of the relationship between body length and jumping performance in *Ascaphus truei*, *Bufo americanus*, *Dendrobates auratus*, and *Acris gryllus*. (Lines are linear regression curves; equations and correlation coefficients listed in Table 3.)

found that larger individuals have proportionately shorter jumps than those of smaller individuals. Dobrowolska (1973) also showed in her species samples with both juveniles and adults that juveniles are better jumpers than adults (Table 4). A subset of my samples were similarly tested for a correlation between body length and jumping ability (Table 5 and Figure 3). This subset includes both those species with a high correlation between length and actual jumping distance and those with no or low correlation. The low correlation species (*B. americanus*, *C. inguinalis*, *A. gryllus*, *E. martini-*

censis, and *G. carolinensis*) show, as a whole, greater slopes of the regression curve than do the high correlation species. Nonetheless, the general trend in both groups is the same: Smaller individuals tend to jump farther relative to their body length than do larger individuals. The differences in jumping ability are not great. *Acris* has the greatest slope with 0.38, but in most cases the slope is nearly 0. Thus, although smaller individuals are stronger jumpers than larger individuals, the difference is not significant in most species.

The comparison of body length to relative jump-

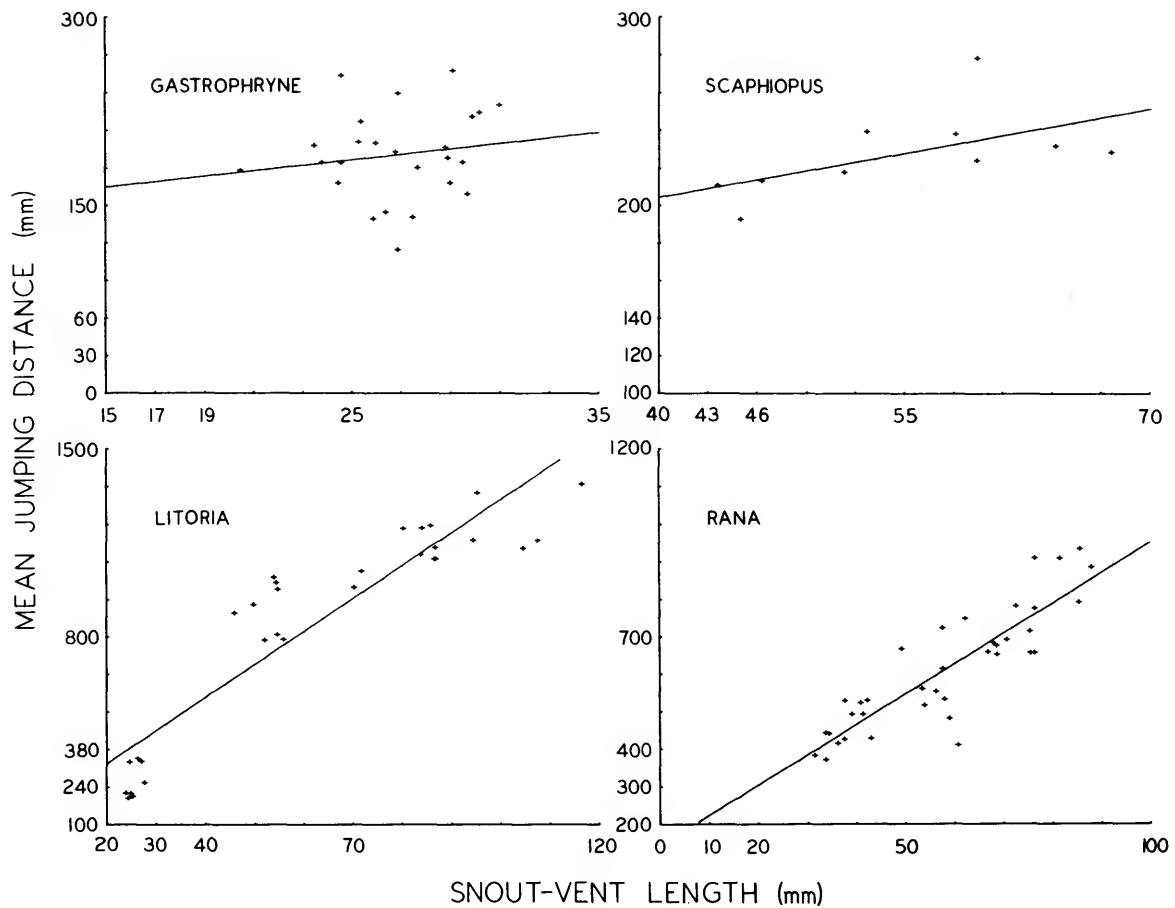


FIGURE 2.—Examples of the relationship between body length and jumping performance in *Gastrophryne carolinensis*, *Scaphiopus couchi*, *Litoria infrafrenata*, and *Rana clamitans*. (Lines are linear regression curves; equations and correlation coefficients listed in Table 3.)

ing ability was also tested by power (Table 5), parabolic, and exponential regression analyses. As in the previous comparisons of length and actual jumping distances, the power equations describe the trend of points equally as well as the linear equations. The exponential and parabolic equations' correlation coefficients are also similar and only in *Litoria infrafrenata* did the parabolic equation ($Y = 2.76 + 0.40 - 0.003X^2$, $r = 0.72$) describe the trend better than the linear or power equations. The smallest *infrafrenata* were metamorphs with tail stubs remaining or recently reabsorbed and they were poorer jumpers than juveniles or adults.

Although the preceding paragraphs have dis-

cussed the relationship of jumping performance and body length, the conclusions can just as well be applied to age, because snout-vent length can be used as an estimator of age. The data suggest the following two generalizations: (1) the actual jumping distance of a frog is directly proportional to its body length or any other body measurement that increases with age; (2) the relative jumping ability of a frog decreases with increasing body length, but only slightly. The effect of size on jumping performance can also be studied by examining the relationship between weight and jumping distance (Table 6, Figure 4). The same trend of increasing jumping length with increasing weight is still apparent,

TABLE 4.—A comparison of the relative jumping ability of juvenile and adult European frogs (data recalculated from Dobrowolska, 1973; RJA = mean jumping ability, SV = mean snout-vent length, mm)

Taxon	Juveniles		Adults	
	SV	RJA	SV	RJA
<i>Bufo bufo</i>	23.3	3.6	77.4	1.5
<i>Bufo viridis</i>	34.8	3.4	64.1	2.5
<i>Bombina bombina</i> ...	20.5	4.6	40.7	3.8
<i>Rana arvalis</i>	27.4	8.2	59.1	6.6
<i>Rana esculenta</i>	25.5	9.8	66.5	5.6
<i>Hyla arborea</i>	23.9	8.1	41.0	9.8

although the scatter of the points is somewhat greater. The power equation is usually the best descriptor of this trend. Only in the male *R. catesbeiana* sample is a different trend dominant; the subadults and small adults are better jumpers than the juveniles and large adults. I believe this to be an artifact of testing that shows low motivation on part of the frogs, i.e., I was not a terrifying predator for large adults.

SEX.—The sex of an individual may affect its jumping performance. My assumption is that immature individuals of both sexes would have the

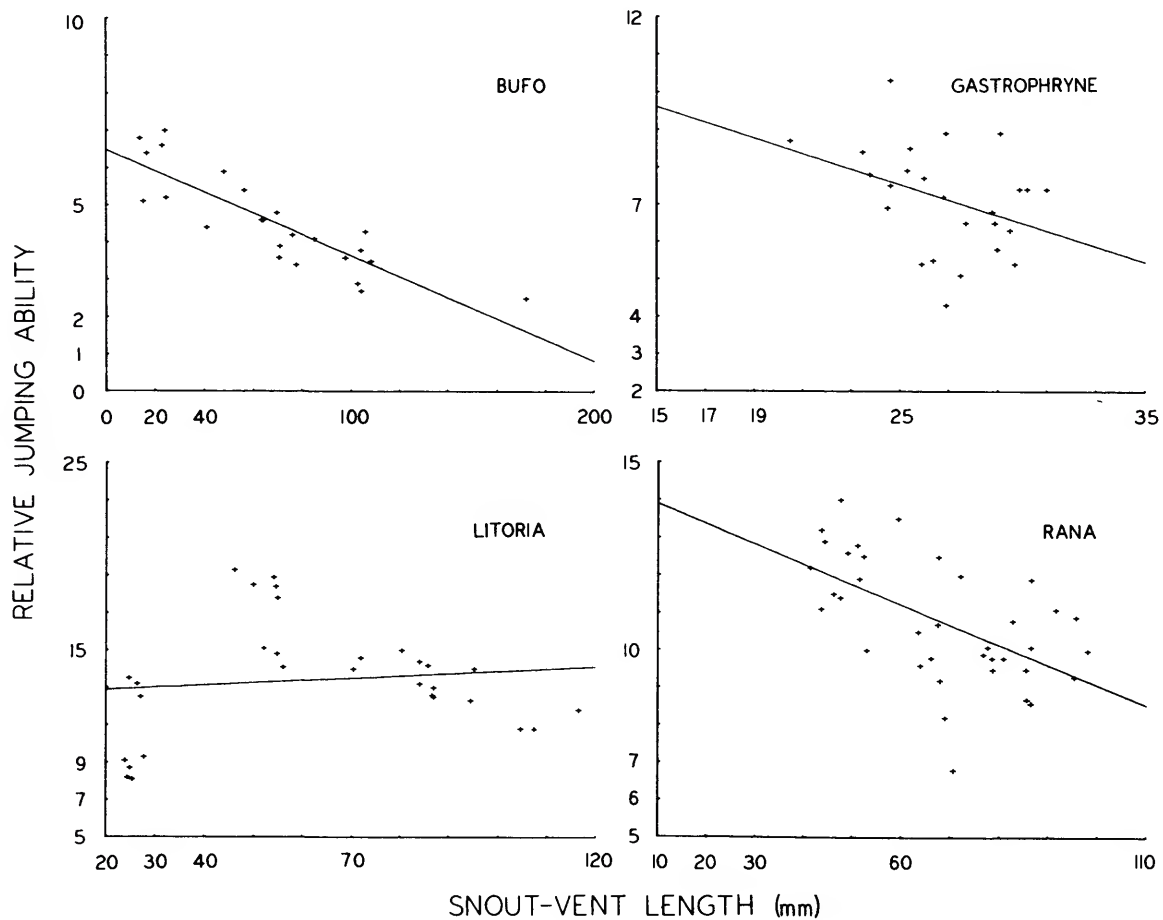


FIGURE 3.—Examples of the relationship between body length and relative jumping ability in *Bufo marinus*, *Gastrophryne carolinensis*, *Litoria infrafrenata*, and *Rana clamitans*. (Lines are linear regression curves; equations and correlation coefficients listed in Table 5.)

same jumping ability, but as sexual maturity is reached the divergence of morphology, physiology, and endocrinology—even though they may be minor—would alter the jumping performance of the two sexes. The most obvious variables affecting differential performance are length differences in sexually dimorphic species, disproportionate weight increase of gravid females, fatigue in calling

males due to low food intake and high activity, differential reaction to stimuli due to different endocrine titers, and differential selection for predator responses.

A subset of specific samples, which possess a wide size range and nearly equal numbers of both sexes, were selected for analysis (Tables 6, 7; Figures 4, 5) to discern sexual differences. The adult females

TABLE 5.—The effect of size (snout-vent length, X, mm) on relative jumping ability (mean jumping distance divided by snout-vent length, Y, mm) in 10 species of frogs as shown by linear and power regression equations (abbreviations the same as in Table 3)

Taxon	LINEAR			POWER		
	A	B	r	A	B	r
A. truei.....	17.07	-0.06	-0.36	25.58	-0.15	-0.35
B. americanus.....	5.75	-0.03	-0.49*	23.66	-0.46	-0.49*
B. marinus (PNG).....	6.48	-0.03	-0.85*	17.13	-0.34	-0.84*
C. inguinalis.....	22.86	-0.36	-0.51*	87.05	-0.57	-0.51*
A. gryllus.....	15.80	0.38	0.14	7.10	0.39	0.21
E. martinicensis.....	17.79	-0.32	-0.58*	129.57	-0.82	-0.62*
G. carolinensis.....	12.71	-0.21	-0.37	82.81	-0.75	-0.35
L. infrafronata.....	12.64	0.01	0.12	6.93	0.16	0.35
R. clamitans.....	13.89	-0.05	-0.57*	32.91	-0.28	-0.57*
R. grisea.....	20.40	-0.05	-0.53*	26.77	-0.12	-0.43*

TABLE 6.—A comparison of the relationship between weight (X, g) and jumping distance (Y, mm) in seven species of frogs (N = number of individuals, B = slope of regression curve, r = correlation coefficient)

Taxon	N	Linear		Parabolic		Exponential		Power	
		B	r	B	r	B	r	B	r
B. americanus									
♂.....	17	1.80	.42	1.76	.42	0.01	.42	0.16	.47
♀.....	14	2.07	.71*	2.11	.71*	0.01	.68*	0.18	.63*
D. auratus									
♂.....	10	43.18	.65*	43.23	.65*	0.35	.67*	0.49	.74*
♀.....	13	24.04	.68*	24.20	.68*	0.16	.69*	0.27	.74*
A. gryllus									
♂.....	14	229.48	.20	229.48	.22	0.32	.20	0.26	.20
♀.....	14	227.06	.66*	227.05	.66*	0.58	.67*	0.43	.74*
O. septentrionalis									
♂.....	10	6.76	.20	7.06	.20	.01	.17	0.05	.14
♀.....	15	2.34	.20	1.66	.17	.00	.22	0.12	.41
L. infrafronata									
♂.....	21	-0.55	-.30	-0.66	-.30	-.00	-.70*	0.03	.05
♀.....	16	7.17	.79*	6.60	.78*	.01	.70*	0.39	.91*
R. catesbeiana									
♂.....	9	0.93	.55	7.12	.88*	.00	.57	0.17	.73*
♀.....	11	0.92	.66*	2.71	.79*	.00	.71*	0.17	.84*
R. utricularia									
♂.....	12	22.74	.58*	22.41	.58*	.04	.66*	0.32	.70*
♀.....	11	6.59	.60*	6.14	.60*	.01	.66*	0.24	.76*

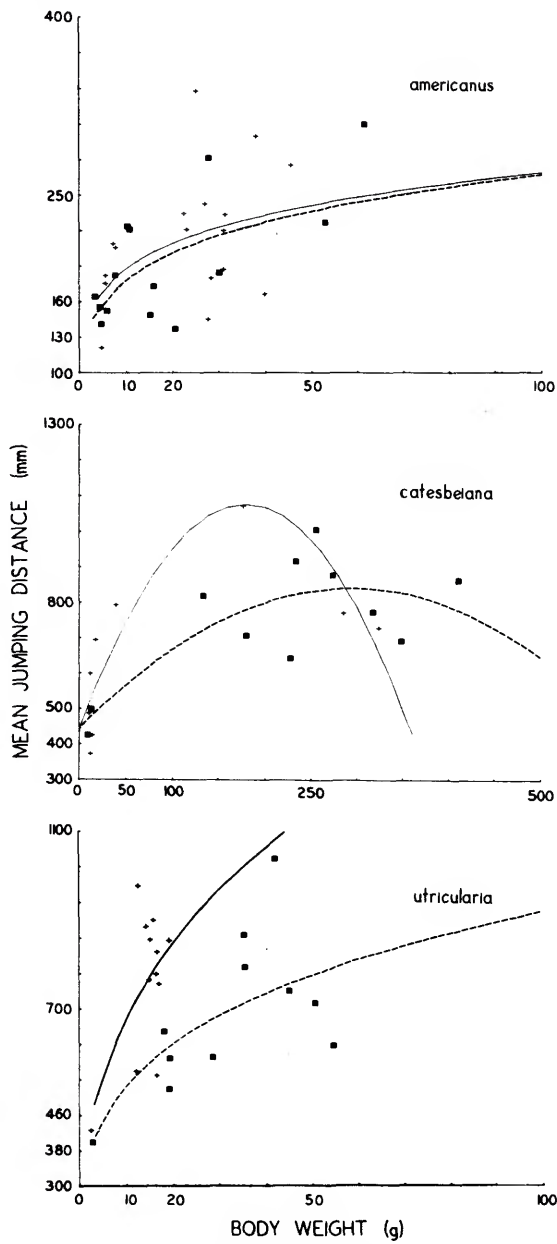


FIGURE 4.—Examples of the relationship between weight and jumping performance in female and male *Bufo americanus*, *Rana catesbeiana*, and *R. utricularia*. (Males designated by crosses and solid lines, females by squares and broken lines; lines are power regression curves for A and C and parabolic regression curves for B; other data presented in Table 6.)

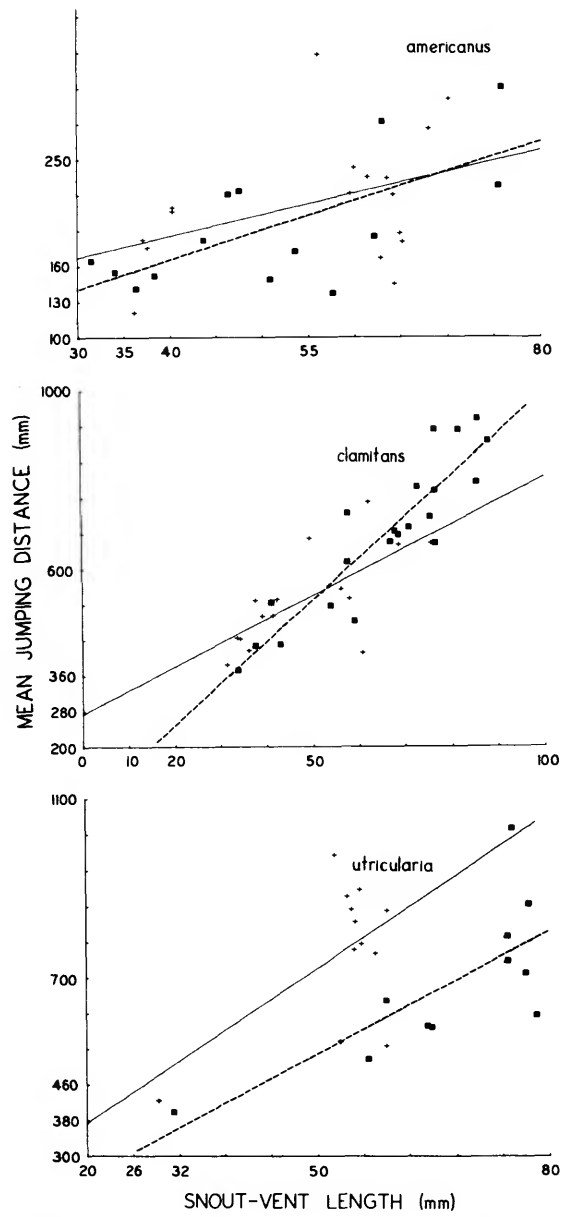


FIGURE 5.—Examples of the relationship between body length and jumping performance in female and male *Bufo americanus*, *Rana clamitans*, and *R. utricularia*. (Lines are linear regression curves; crosses and solid lines designate males, squares and broken line females; data from Table 7.)

in *D. auratus*, *L. caerulea*, and *R. utricularia* samples were predominantly gravid; only an occasional female was gravid in the other samples. The adult males in all samples except *D. auratus* were actively engaged in reproductive activities. An intraspecific comparison of the relationship of body length to jumping distance (Table 7) reveals that only the samples of the *B. americanus*, *D. auratus*, *R. clamitans*, and *R. utricularia* samples have linear correlation coefficients, which are roughly equivalent between the sexes and are statistically significant. For the relationship of weight to jumping distance, the *B. americanus*, *D. auratus*, *R. catesbeiana*, and *R. utricularia* samples are roughly equivalent between the sexes and are statistically significant. In the other specific samples, the correlation coefficient is low for both sexes or, at least for one of the sexes, thus making them unreliable estimators of the influence of sex on jumping ability.

Sexual differences are apparent in the body length to jumping distance analysis for *D. auratus*, *R. clamitans*, and *R. utricularia*; *B. americanus* demonstrates no sexual dimorphism. The adult female *clamitans* are jumping farther than equivalent sized males. Adult female *auratus* jump more poorly than equivalent size males according to the slope of the linear regression curve. However an examination of the scatter of points indicates there is no actual difference in the performance of females and males, since a single linear regression curve (see Table 3) for both sexes describes the relationship equally as well as separate curves. The difference between the sexes of *R. utricularia* are quite strik-

ing; females of all age classes are poorer jumpers than are males. Although this behavioral difference may reflect an actual difference in jumping ability, the small sample size and the gravid condition of five of the largest individuals leaves such a conclusion tenuous.

The weight to jumping distance relationship (Table 6 and Figure 4) shows no sexual dimorphism for *B. americanus* and *R. catesbeiana*; their linear and power regression curves for the sexes are nearly identical. *Dendrobates auratus* and *R. utricularia* display striking sexual dimorphism. Although the analysis shows adult female *auratus* to be poorer jumpers than males of an equivalent weight, the scatter of the points show that a single curve for both sexes would have as high or higher a correlation coefficient than the curves for separate sexes. In *R. utricularia*, weight possesses the same relationship to jumping distances as does body length; females are the poorer jumpers.

The data for *C. nubicola*, *D. auratus*, *O. septentrionalis*, *E. martinicensis*, *C. cryptotympanum*, and *R. utricularia* show a poorer jumping ability for adult females. Since the adult female *auratus* and *utricularia* are mostly gravid, this leads to the conclusion that the increased weight of the developing ova and, perhaps, a different physiological and hormonal state decrease the jumping ability of females or the effect of landing force on developing ova placed a selective premium on females with shorter jumps. However, the three other species show no sexual dimorphism or the reverse trend. In fairness, I can conclude only that adult females

TABLE 7.—A comparison of the effect of sex on the relationship between size and jumping performance; the data are from linear regression analyses (N = number of specimens tested; other abbreviations the same as in Table 3)

Taxon	Males				Females			
	N	A	B	r	N	A	B	r
<i>B. americanus</i>	17	113.21	1.80	.40	14	65.99	2.48	.67*
<i>C. nubicola</i>	9	-2.19	15.34	.71*	12	260.00	-2.71	-.10
<i>D. auratus</i>	10	-59.68	8.77	.75*	13	47.09	4.78	.74
<i>A. gryllus</i>	14	249.62	13.93	.10	14	-85.11	25.24	.68
<i>O. septentrionalis</i> ...	10	346.81	7.61	.35	15	609.40	3.52	.28
<i>E. martinicensis</i>	7	366.37	-6.58	-.36	7	484.36	-7.19	-.61
<i>C. cryptotympanum</i>	9	307.77	2.06	.10	8	1106.25	-23.04	-.74*
<i>L. caerulea</i>	12	647.79	-0.90	-.10	11	431.65	1.49	.20
<i>R. clamitans</i>	16	273.64	5.31	.69*	21	62.79	9.33	.91*
<i>R. utricularia</i>	12	143.14	11.53	.55*	11	69.38	9.18	.74*

tend to be poorer jumpers. More experiments are necessary to confirm sexual dimorphism in jumping ability and to determine the factors that cause the differential performance.

FATIGUE.—Muscular activity in anurans is largely energized by anaerobic glycolysis. Presumably the resulting build-up of lactic acid and the increasing oxygen debt would put a premium on a strong first jump to escape from a predator. Succeeding jumps would become progressively shorter as muscular fatigue developed. The available evidence neither confirms nor negates a progressive deterioration of jumping performance. Although not tests for fatigue, a comparison of Wermel's (1934) and Dobrowolska's (1973) data (Table 1) show that the mean jumping distances of frogs jumping fifty times in succession are quite similar to those of frogs jumping only 10 times. In tests for endurance, Rand (1952) found that, even though the individual jumps of strong jumping frogs (*A. crepitans*, *H. crucifer*, *P. triseriata*) vary widely over a series of 30 to 120 jumps, a decline in jumping performance does occur with an occasional jump later in the series nearly equivalent to earlier strong jumps. More importantly, he noted that after the first several leaps these frogs were reluctant to continue

jumping and attempted to hide. In contrast, weak jumpers (*B. fowleri*) showed no decline in jumping performance and no reluctance to continue jumping.

During my initial jumping tests, I had each frog jump five times each for five trials. In spite of the brief resting period (approximately two minutes) between each trial as I measured the previous jumps, I noted a reluctance to jump in the later trials and presumably a decrease in jumping performance. Thus, these data provide an opportunity to test further the endurance or jumping fatigue of frogs. The data were examined by a one-factor analysis of variance with the jumping trials as factors. In the strict statistical sense, the results may be considered unreliable since the same individuals were used for each trial and, thus, the trials or factors are not independent; however, in the biological sense, this dependency of successive trials is required for testing of the development of fatigue.

The results are displayed in Table 8 and Figure 6. Only in *Acris gryllus* are the ANOVA results statistically significant with a progressive decline in jumping performance. Other species (*Hyla crucifer*, *H. regilla*, *Rana clamitans*, *R. virgatipes*) also show poorer jumping performance in successive trials. In

TABLE 8.—A comparison of mean jumping distance in five successive trials of five jumps each (N = number of individuals tested, I-V = successive trials, F = F ratio for a one-factor ANOVA, * = significant probability at 0.05 level)

Taxon	N	I	II	III	IV	V	F
<i>B. americanus</i>	6	201	200	189	201	197	0.09
<i>B. boreas</i>	5	255	246	254	243	242	0.07
<i>B. fowleri</i>	12	234	242	243	233	245	0.08
<i>B. microscaphus</i>	6	241	236	242	223	223	1.96
<i>B. punctatus</i>	8	177	195	185	175	182	0.43
<i>B. quercicus</i>	5	73	74	72	70	76	0.26
<i>B. terrestris</i>	23	203	208	200	195	192	0.87
<40 mm.....	6	185	186	182	175	173	0.16
>55 mm.....	5	206	217	208	213	207	0.33
<i>A. gryllus</i>	19	505	444	369	339	309	6.82*
<i>H. cinerea</i>	6	516	527	554	527	564	0.29
<i>H. crucifer</i>	26	533	506	490	468	453	2.97
<i>H. femoralis</i>	25	390	419	436	418	432	1.07
<i>H. regilla</i>	9	451	402	390	366	345	3.22
<i>H. versicolor</i>	17	410	410	375	375	364	1.17
<i>S. holbrooki</i>	4	179	192	177	174	172	0.36
<i>R. catesbeiana</i>	8	688	703	707	652	626	0.16
<i>R. clamitans</i>	21	620	583	558	501	513	2.31
<40 mm.....	6	449	426	405	375	381	1.48
>70 mm.....	6	828	756	718	649	644	3.20
<i>R. dalmatina</i>	4	536	459	537	499	532	0.22
<i>R. virgatipes</i>	14	331	330	304	278	273	3.38

contrast to these strong jumpers, the weak jumpers (*Bufo* and *Scaphiopus*) show a nearly equivalent performance in successive trials or, at most, a slight decline. While this is in general agreement with the findings of Rand (1952), a generalization cannot be made that strong jumpers tire faster than weak

jumpers since several of the strong jumpers possessed the same endurance pattern as weak jumpers (e.g., *H. versicolor*, *R. dalmatina*) or showed an improved performance (e.g., *H. cinerea*, *H. femoralis*). I suspect that this lack of uniformity among the stronger jumpers results from two factors: the rest

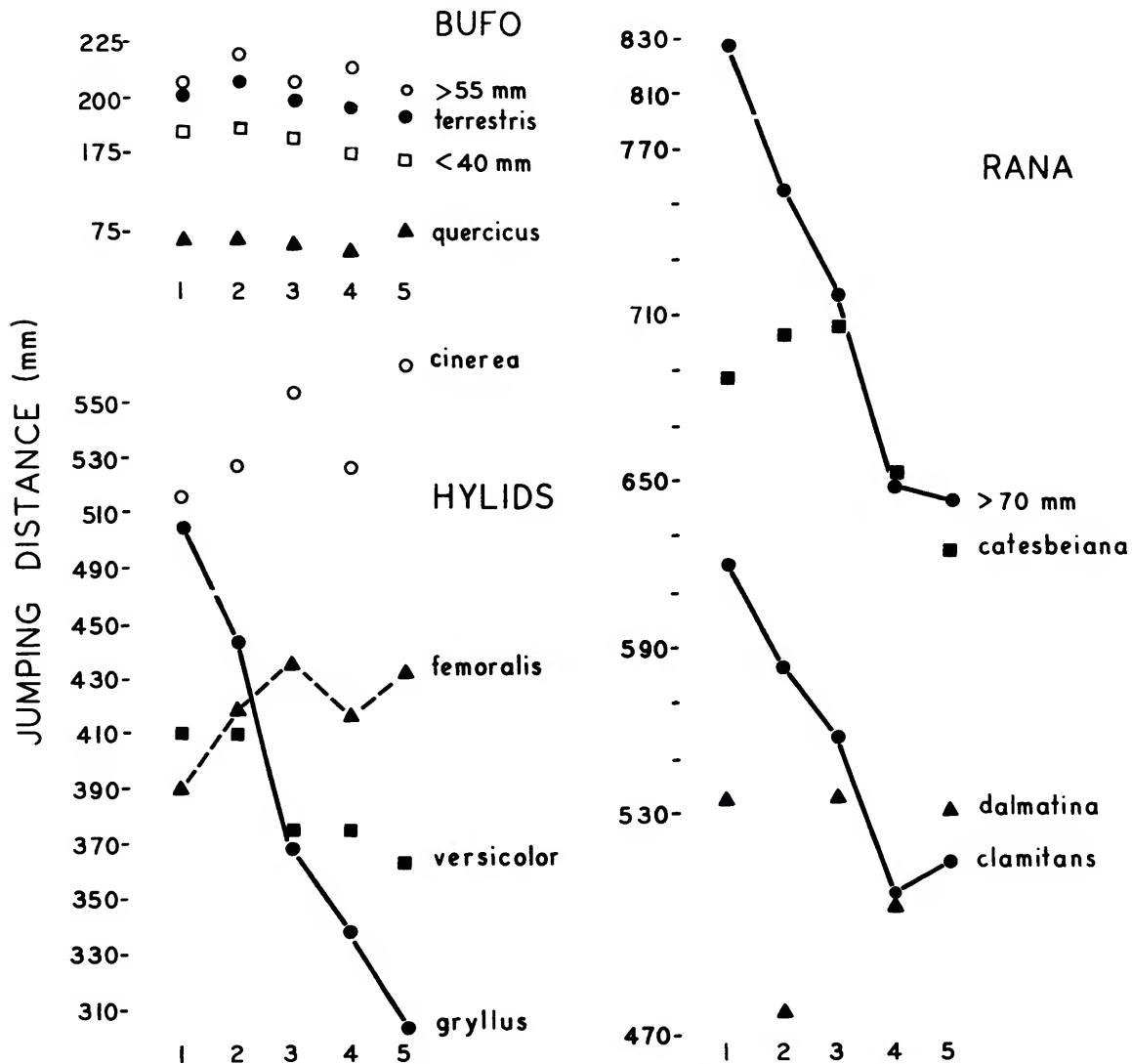


FIGURE 6.—Jumping endurance as shown by the mean jumping distance of frogs for five successive trials: *Bufo terrestris* (all sizes; snout-vent length greater than 55 mm and less than 40 mm), *B. quercicus*, *Hyla cinerea*, *H. femoralis*, *H. versicolor*, *Acris gryllus*, *Rana catesbeiana*, *R. clamitans* (all sizes; body length greater than 70 mm), and *R. dalmatina*.

period between successive trials and the influence of body size on jumping performance. Rand (1952) observed that a two or five minute rest period restored jumping performance in a sample of two *H. crucifer*. A rest period is likely to restore an individual's jumping capabilities for the initial few leaps, but a faster deterioration in performance in successive trials would be expected. This trend is evident in all the strong jumpers except *H. cinerea*, *H. femoralis*, and *R. dalmatina*. This trend in strong jumpers and the uniformity of jumping performance in the weak jumpers indicates a different muscular energetic system in the two groups. The discovery of a high aerobic scope in *Bufo boreas* (Bennett and Licht, 1973) supports this supposition.

Size or age may influence jumping performance. In the hylids (Table 9), there is a weak trend of increased endurance with increasing body size. *Acris gryllus*, the smallest hylid species tested, possesses the least endurance. This species also has the highest relative jumping ability (Table C of Appendix), which suggests a greater muscular effort and energy expenditure per jump, a possible reason for a faster onset of fatigue. A comparison of the relative jumping ability for the other hylid species does not support a trend of increasing endurance with decreasing ability. Excluding the juvenile *Rana clamitans* from the ranid comparison (Table 9) reveals an opposite trend with increasing endurance as a species body size decreases. Whether this trend would continue if extended into hylid body size range or a reversal of the hylid trend would occur if extended into ranid body size range is unknown. The juvenile *R. clamitans* sample might be used as evidence for a reversal, thereby suggesting that each genus, perhaps each species, possesses an optimum body size at which endurance is maximized and on either side of which endurance decreases. However, such a

statement at this time is purely conjecture.

HABITAT.—Do the anuran species adapted to a similar habitat or sharing a similar life style also possess a similar jumping ability? To answer this question, I divided the frogs into three gross categories: semiaquatic, terrestrial, and arboreal (these are equivalent to terrestrial III, terrestrial I-II, and arboreal I-III, respectively, which are defined later in the text). All three groups (Table 10, Figure 7) possess a significant positive correlation between body size and maximum jumping ability. The regression curve, whether linear or power, has a low negative slope indicating a slightly better jumping ability of the smaller species. However, the scatter in the graph is large, and in spite of the significance of the linear correlation coefficients, the regression curves are accounting for only 25% or less of the variance. This is too low to form any definite conclusions. A one-factor analysis of variance shows that the means for the three categories are not significantly different (F ratio = 6.04, df = 2/77). About all that can be said is that semiaquatic frogs have a relative jumping ability of 13.1, 7.0–23.4 (mean) and 15.9, 8.5–31.4 (maximum), terrestrial frogs 10.4, 3.1–25.4 (mean) and 12.5, 3.8–29.0 (maximum) and arboreal frogs 15.4, 7.8–24.4 (mean) and 17.7, 8.4–29.4 (maximum).

Since the association between jumping ability and these three habitat groups show considerable variation, I decided to further subdivide the habitat preferences into groups that might be more accurate indicators of niche. The terrestrial and arboreal habitats were each divided into three units. The first (I) terrestrial group includes those anurans living on dry or well-drained soil with an open or closed canopy; they are usually found around or in water only during the breeding season and they tend to be fossorial or partially so. Terrestrial I con-

TABLE 9.—The relationship of body length and the difference between jumping performance in first and fifth jumping trials (same sample sizes as in Table 8, SV = mean snout-vent length of the specimens in the five trial samples)

Taxon	Difference	SV		Difference	SV
<i>A. gryllus</i>	-196	20.7	<i>R. clamitans</i>		
<i>H. regilla</i>	-106	35.9	>70 mm.....	-184	91.9
<i>H. crucifer</i>	-80	27.0	<40 mm.....	-68	36.0
<i>H. versicolor</i>	-46	43.5	<i>R. catesbeiana</i> ...	-62	91.7
<i>H. femoralis</i>	42	29.0	<i>R. virgatipes</i>	-58	46.9
<i>H. cinerea</i>	48	46.4	<i>R. dalmatina</i>	-4	46.6

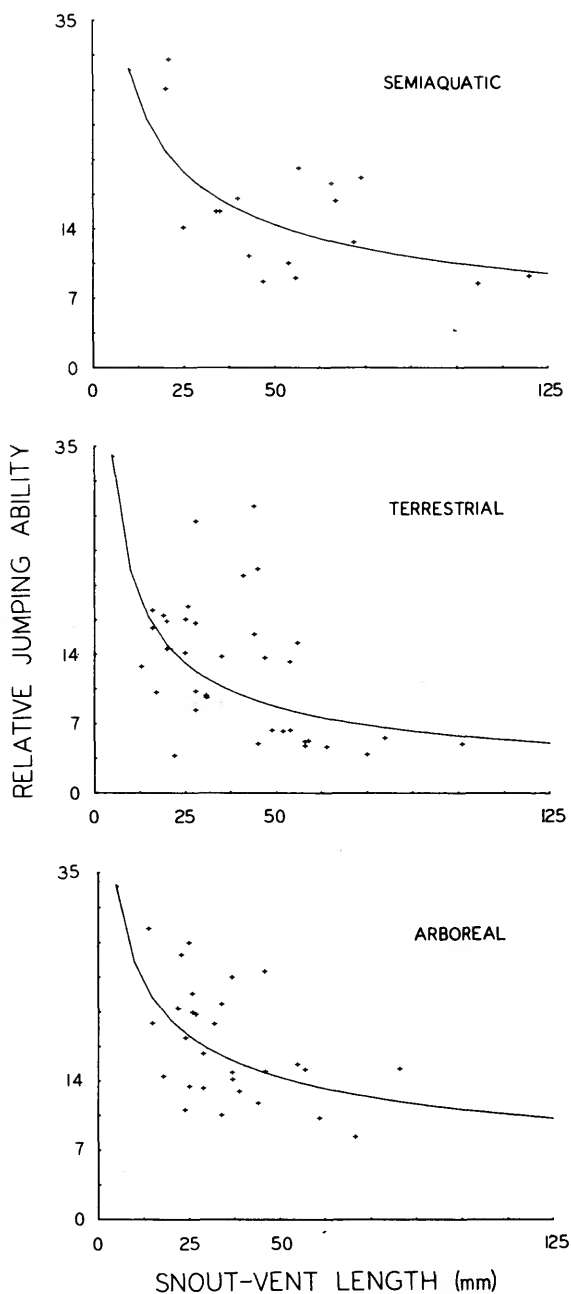


FIGURE 7.—Association of maximum jumping ability and body size (mean for adult males) in semiaquatic, terrestrial, and arboreal frogs. (Linear and power regression equations same as in Table 9.)

tains all *Bufo* and *Scaphiopus*, *Gastrophryne carolinensis*, and *Pherohapsis menziesi*. The terrestrial II group live in damp to dry situations (seepage areas to moist woodland or grassland) with an open or closed canopy; they are not fossorial. Terrestrial II contains *Colostethus nubicola*, *C. sp.*, *C. pratti*, *C. trinitatis*, all *Dendrobates* and *Pseudacris*, *Eleutherodactylus cochranae*, *E. lentus*, *E. planirostris*, *Leptodactylus albilabris*, *Lechriodus melanopyga*, *Litoria nasuta*, *Platymantis papuensis*, *Rana dalmatina*, *R. palustris*, *R. sylvatica*, and *R. utricularia*. The terrestrial III group live in damp to wet situations (borders of or in streams and lakes, marshes and swamps); they are not fossorial and many are excellent swimmers. Terrestrial III contains *Ascaphus truei*, *Colostethus inguinalis*, *Discoglossus pictus*, both *Acris*, *Hyla arenicolor*, *H. regilla*, *Sphenophryne palmipes*, *Rana aurora*, *R. catesbeiana*, *R. clamitans*, *R. grisea*, *R. grylio*, *R. papua*, *R. virgatipes*, and *Rana* species. The low mean jumping ability of terrestrial I (4.7) as compared by one-factor ANOVA to terrestrial II and III (13.6 and 13.1) is not significantly different but nearly so ($F = 19.3$, $df = 2/50$).

The arboreal groups do not discriminate on the presence or absence of water beneath the supportive structures or its presence or absence in microenvironments, e.g., bromeliads, in or on the supportive structures. Arboreal I is a grass or reed environment with open or partially open canopy; *Limnaeodius ocularis*, *Eleutherodactylus brittoni*, *Litoria bicolor*, *L. caerulea*, and *L. impura* are members of this group. Arboreal II includes anurans living in shrubs or low in trees and contains *Hyla andersoni*, *H. cinerea*, *H. crucifer*, *H. squirella*, *Eleutherodactylus antillensis*, *E. coqui*, *E. locusta*, *E. martinicensis*, *E. portoricensis*, *Cophixalus cryptotympanum*, *Litoria angiana*, *L. congenita*, *L. micromembrana*, *L. nigropunctata*, *L. thesaurensis*, and *L. vocivincens*. Arboreal III contains those species living at medium to high levels in trees; they are *Hyla chrysoscelis*, *H. femoralis*, *H. gratiosa*, *H. versicolor*, *Osteopilus septentrionalis*, *Eleutherodactylus hedricki*, and *Litoria infrafrenata*. The mean jumping ability of these three arboreal groups (19.1, 15.7, and 11.5) are not significantly different ($F = 4.0$, $df = 2/26$).

The finer definition of habitat groups improves the analysis only slightly (Figure 8 and Table 10). Only three groups show particularly meaningful

TABLE 10.—The relationship between body size (mean snout-vent length of adult males, X, mm) and maximum relative jumping ability (Y, mm) in frogs of different habitat preference (N = number of specimens tested; other abbreviations the same as in Table 3)

Taxon	N	Linear			Power		
		A	B	r	A	B	r
Semiaquatic.....	17	22.65	-0.13	-.53*	86.27	-0.46	-.60*
Terrestrial.....	36	18.86	-0.16	-.47*	88.22	-0.59	-.51*
Arboreal.....	29	23.39	-0.15	-.46*	61.18	-0.37	-.49*
Terrestrial							
I.....	14	7.83	-0.04	-.45	14.09	-0.24	-.37*
II.....	22	14.91	0.06	.15	11.17	0.11	.16
III.....	17	23.45	-0.14	-.58*	102.39	-0.50	-.64*
Arboreal							
I.....	6	29.72	-0.25	-.75*	104.07	-0.50	-.70*
II.....	16	19.82	-0.06	-.11	19.03	-0.02	-.03
III.....	7	12.62	-0.01	-.10	12.41	0.01	.03

relationship between jumping ability and size. The terrestrial I and arboreal III groups have low slopes that are probably not significantly different and despite low correlation coefficients the scatter or variance of points along the regression curves is slight; their relative jumping abilities are 4.7, 3.1–7.2 (mean), 5.8, 3.8–10.3 (maximum) and 11.5, 8.6–13.6 (mean), 13.3, 10.3–16.8 (maximum), respectively. No matter how large or small the species, they possess the same jumping ability. The terrestrial I members are hoppers; they have short jumps and high endurance, thereby permitting high mobility. Perhaps the moderate jumping ability of arboreal III members may reflect a compromise between high mobility in the treetops and the inherent danger of this unstable environment, e.g., longer jumps, less accuracy, a fall more likely. Terrestrial III shows the distinct trend for decreasing jumping ability with increasing size. Undoubtedly this is due in part to the proportionately faster increase in weight with increasing length, but also may reflect the tendency of larger species to sit closer to water and use a single jump into water as the major escape behavior. The relative jumping ability of terrestrial III members is 14.0, 7.6–23.4 (mean) and 16.0, 8.5–31.1 (maximum).

Trends in the other three groups are not evident because of high variance or small sample size. The relative jumping ability of the terrestrial II members is 14.1, 6.5–25.4 (mean) and 16.8, 9.7–29.0 (maximum), for arboreal I members 18.8, 7.8–24.4 (mean) and 21.8, 8.4–29.4 (maximum), and for arboreal II members 15.7, 9.4–25.6 (mean) and 18.1,

11.1–28.0 (maximum). The major point illustrated by these data is that a definite correlation between jumping ability and habitat or niche does exist, but the preceding approach is too simplistic. A more discriminating analysis is planned and shall consider a larger variety of environmental and behavioral variables.

TAXONOMY.—An appraisal (Table 11, Figure 9) of the intrafamilial variation of jumping ability reveals two general trends. The bufonids have a direct relationship between body size and jumping. Large species not only jump farther than their smaller congeners, but they also jump proportionately farther. However, the difference in ability between the smallest and largest toad species is slight (3.3 and 4.6, respectively) and not statistically significant. Toads are the poorest jumpers of all the frogs. Presumably they have traded high performance for energy conservation in their locomotion. Jumping is obviously no longer the first line of defense against predator attack.

All other anuran families show an inverse relationship between body size and jumping. Smaller species are better jumpers—relatively—than their bigger congeners. This is exactly the same trend as observed intraspecifically where juveniles are relatively better jumpers than adults. Both cases are probably the result of the threefold increase in weight with a doubling of length. In all families, there is little difference in the regressions of mean and maximum jumping ability; the slopes of mean and maximum curves are nearly identical in all except the leptodactylids, which show a faster de-

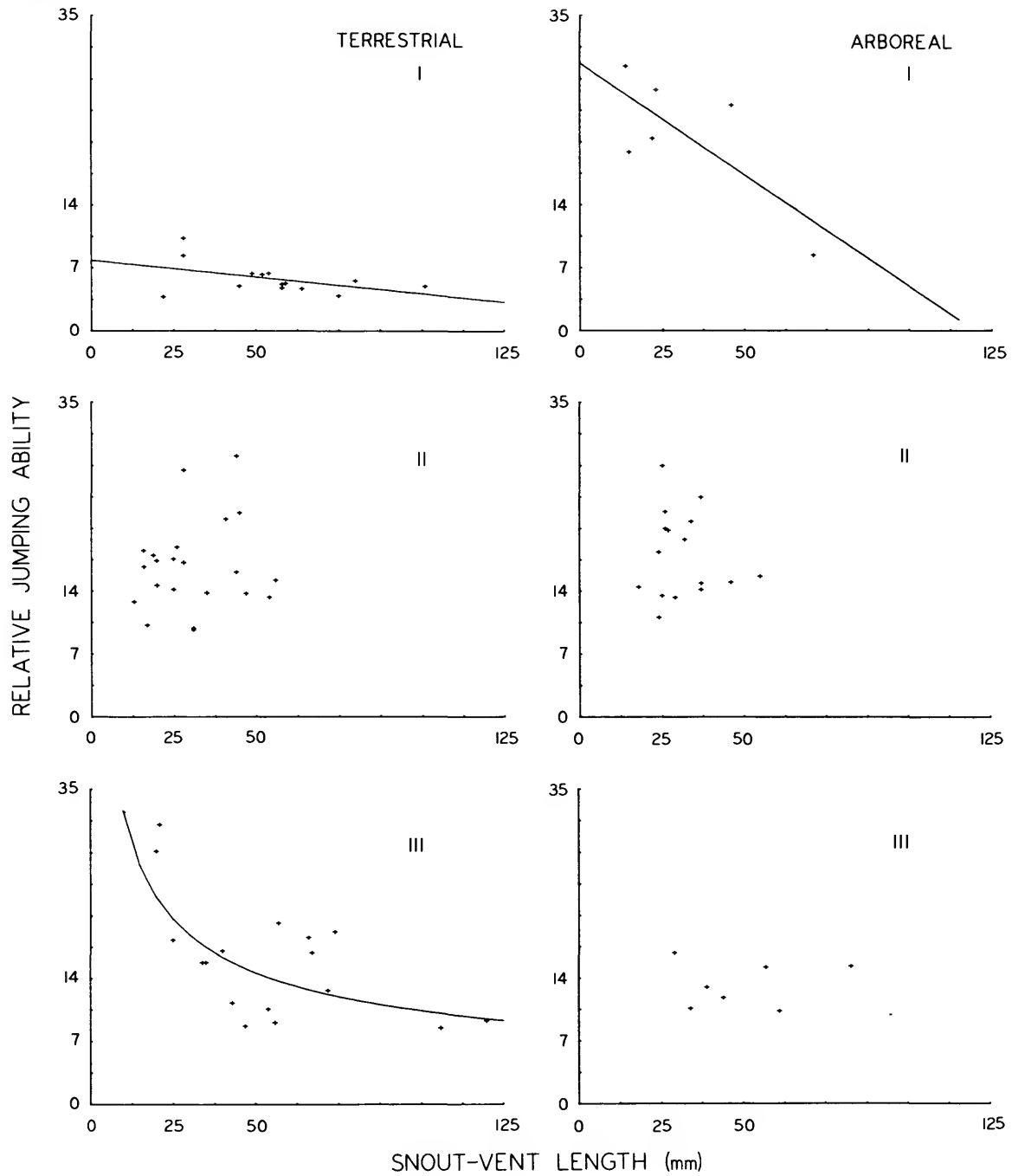


FIGURE 8.—Association of maximum jumping ability and body size (mean for adult males) in frogs of different habitat preference. (Linear and power regression equations same as in Table 9; definitions of habitat groups terrestrial, I-III, and arboreal, I-III, and their species composition are presented in text.)

TABLE II.—A comparison between the body size of a species (mean adult male snout-vent length, X, mm) and relative jumping ability (mean and maximum, Y, mm) in seven families of frogs (the regression equation, linear (L) or power (P), with the highest correlation coefficient was selected for presentation)

Taxon	Regression Equation	Mean			Maximum		
		A	B	r	A	B	r
Bufonidae.....	P	2.52	0.12	.32	2.75	0.14	.38
Dendrobatidae.....	L	16.18	-0.19	-.33	20.11	-0.22	-.38
Hylidae.....	P	128.93	-0.63	-.69*	220.06	-0.74	-.76*
Leptodactylidae.....	L	13.06	-0.07	-.20	17.26	-0.12	-.32
Pelodyridae.....	L	27.68	-0.20	-.72*	29.93	-0.21	-.68*
Ranidae.....	L	17.02	-0.07	-.37	20.11	-0.08	-.44

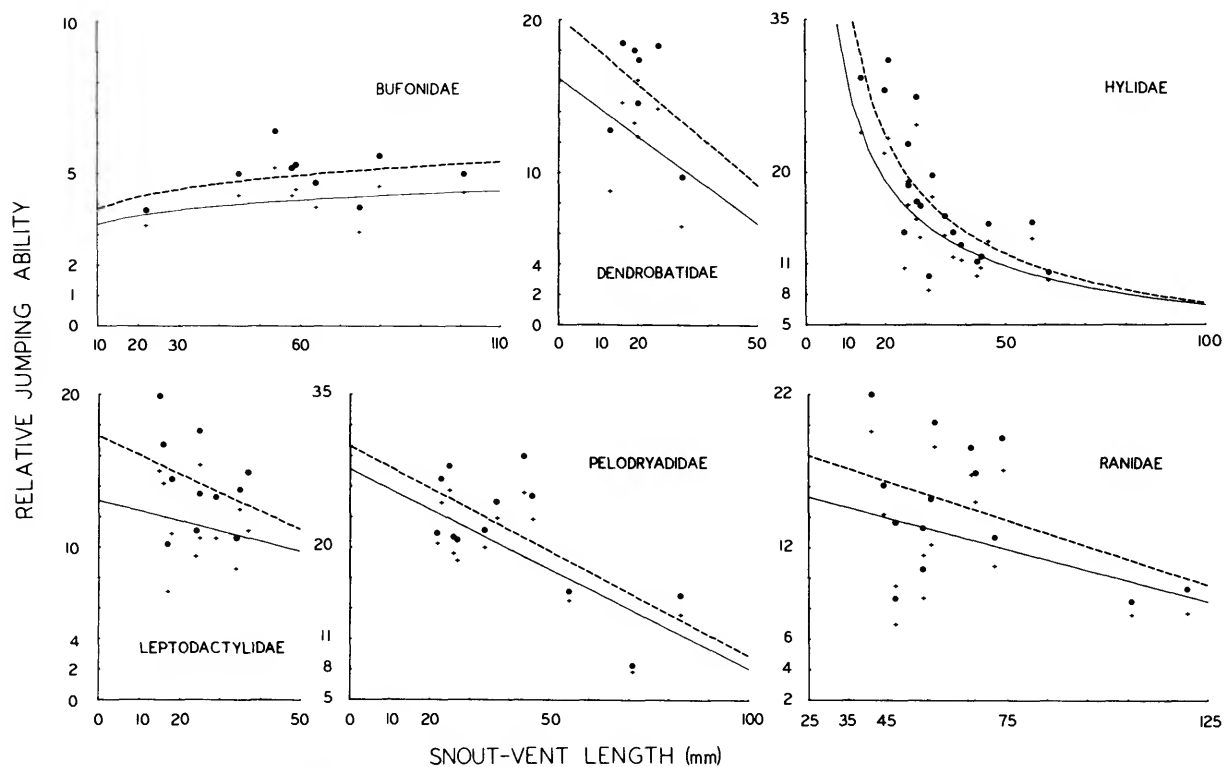


FIGURE 9.—Association of maximum (circles) and mean (crosses) jumping ability and body size (mean for adult males) in six families of frogs.

cline in maximum jumping ability with increasing size.

The pelodyrid tree frogs are somewhat better jumpers than the hylid tree frogs. Medium sized (20–40 mm snout-vent length) pelodyrids have a relative jumping ability in the low 20's in contrast

to the mid teen's for the hylids. It is this difference that accounts for the different shaped curves of these two families. The leptodactylids and ranids share similar slopes and Y-axis intercepts in spite of the dissimilarities in life styles and body sizes of the species in the two samples. The dendrobatids are

most similar to the ranids but possess a steeper slope.

The only conclusions that can be drawn from these data are that the pelodyadids are on the average the best jumpers, the bufonids the worst, and the most common familial trend is a decrease in ability as species' size increases.

Summary

The variation in distances between the successive jumps of a frog can be and often is large. The motivational and physiological state is obviously important in determining a frog's jumping performance, but there is little evidence at present to support this supposition. My observation on decreasing performance with increasing temperature and length of captivity as well as Claussen's (1974) data on effects of desiccation are certainly indicative. Intraspecific variation of equivalent sized individuals appears to be roughly equivalent to intra-individual variation. However, intraspecific variation increases with the addition of all age (size) classes.

The intra-individual variation is a natural component of some species jumping behavior. I have obtained the impression that in some species a pattern of alternating long and short jumps occurs in a sequence of jumps. Whether such patterns are real and whether they are species specific cannot be confirmed by my method of data collection. The patterns will be most evident in the strong jumpers as they show the greatest intra-individual and intra-specific variation. The general trend is an increase in variation with an increase in jumping performance.

Size affects jumping performance. Within a species, the jumping distance increases as the individual grows larger. If the sample contains a wide range of body sizes, it will possess a high positive correlation between jumping performance and body length. Low correlations appear in samples with a limited range of body sizes and thus do not negate the trend of increasing performance with increasing size. However, jumping ability (jumping distance divided by body length) shows an inverse relationship. Juveniles jump proportionately farther than do the adults.

The influence of sex on jumping performance is ambiguous. The general tendency seems to be for

adult males to be stronger jumpers than adult females; however, in two species, the females jumped farther than the males. Since the greater weight of adult females might depress jumping performance, the relationship of body weight to jumping distance was examined and, for the majority of species, males jumped farther than females of equivalent weight.

In a long sequence of jumps, short jumping species jump as far at the end of the sequence as they did at the beginning. Long jumping species usually experience a gradual decline in performance throughout the sequence. The former show no sign of fatigue, whereas the latter demonstrate a gradual onset of fatigue. The fatigue can be relieved by a short rest period. The pattern of alternating jumps may be a fatigue-reducing behavior for strong jumpers as well as a predator-confusing behavior.

In spite of variation in jumping performance and ability in each individual, each species displays a species specific jumping behavior, which is most evident in the reduced variability of the relative jumping ability. At a gross level, terrestrial species have the lowest ability and arboreal species the highest. A finer subdivision of these habitat preferences reveals that of the terrestrial frogs (including the semiaquatic ones), the dry-adapted, semifossorial species are the weakest jumpers, the semiaquatic, nonfossorial species the strongest. In the arboreal frogs, the grass-reed species are the strongest jumpers, the high arboreal ones the weakest. These are only general trends for the correlations between body length and jumping ability are not high. Similar trends and correlations exist in the taxonomic analysis of jumping ability. The earth-bound bufonids and pelobatids are the weakest jumpers, the largely arboreal hylids and pelodyadids the strongest.

For the Guinness world record fans, *Acris gryllus* has the best jumping ability—an average jumping distance of $31.1 \times$ its body length for maximum ability with a high of 61.7. The next closest high was 51.4 for a *Litoria nasuta*. For the longest jump, the honors go to a *Litoria nasuta*, which traveled 2267 mm in a single bound. A *Rana grisea* was a poor second with a leap of 1811 mm. These records fall short of the Guinness' records (McWhirter and McWhirter, 1975), of 5210 mm for a single leap of a *Rana* (presumably *catesbeiana*) or 9675 for three consecutive leaps of a *Ptychadena oxyrhynchus*.

Appendix

Basic Data

TABLE A.—Specimens examined (N = number of individuals in sample; "size range" = minimum and maximum snout-vent length in mm observed in sample; "sex" = number of immature or unsexed individuals/females/males; "locality" = major area from which sample was derived)

Taxon	N	Size Range	Sex	Locality
Ascaphidae				
<i>Ascaphus truei</i>	9	28-48	0/2/7	Washington
Bufonidae				
<i>Bufo americanus</i>	31	32-76	0/14/17	Maryland, Virginia
<i>B. boreas</i>	5	61-103	0/3/2	California
<i>B. fowleri</i>	25	28-70	3/16/6	Maryland, New Jersey, North Carolina
<i>B. marinus</i>	21	72-116	0/3/18	Florida
<i>B. marinus</i>	24	14-172	3/9/12	Papua New Guinea: Central
<i>B. microscaphus</i>	9	47-81	2/4/3	New Mexico, Utah
<i>B. punctatus</i>	8	33-54	1/1/6	Utah
<i>B. quercicus</i>	25	20-26	0/4/21	Florida, North Carolina
<i>B. terrestris</i>	27	27-67	0/11/15	Florida, North and South Carolina
Dendrobatidae				
<i>Colostethus inguinalis</i>	14	19-27	0/6/8	Panama
<i>C. nubicola</i>	21	11-16	0/12/9	Panama
<i>C. sp.</i>	7	12-24	1/2/4	Tobago
<i>C. pratti</i>	6	12-21	1/4/1	Panama
<i>C. trinitatis</i>	4	20-25	0/3/1	Trinidad
<i>Dendrobates auratus</i>	23	17-32	0/13/10	Panama
<i>D. minutus</i>	12	11-15	0/9/3	Panama
Discoglossidae				
<i>Discoglossus pictus</i>	2	56-65	0/0/2	France
Hylidae				
<i>Acris crepitans</i>	24	15-27	0/6/18	Illinois, Louisiana
<i>A. gryllus</i>	28	13-24	0/14/14	Florida, Georgia, North Carolina
<i>Hyla andersoni</i>	2	32-37	0/0/2	New Jersey
<i>H. arenicolor</i>	3	39-46	0/0/3	Utah
<i>H. chrysoscelis</i>	14	30-46	0/1/13	North Carolina, Virginia
<i>H. cinerea</i>	20	29-51	0/5/15	Florida, South Carolina
<i>H. crucifer</i>	36	23-30	0/5/31	Maryland
<i>H. femoralis</i>	27	17-36	1/3/23	Florida, North Carolina
<i>H. gratiosa</i>	2	50	0/1/1	Florida
<i>H. regilla</i>	25	27-43	0/6/19	California
<i>H. squirella</i>	25	27-38	0/2/23	North Carolina
<i>H. versicolor</i>	33	32-54	0/3/30	Indiana, Maryland
<i>Limnaoedus ocularis</i>	15	11-19	1/3/11	Florida, North Carolina
<i>Osteopilus septentrionalis</i> ..	25	43-90	0/15/10	Florida
<i>Pseudacris brachyphona</i>	1	27	0/0/1	Maryland
<i>P. brimleyi</i>	17	25-34	0/3/14	Georgia, Virginia
<i>P. nigrita</i>	11	24-26	0/1/10	Georgia, Mississippi
<i>P. ornata</i>	2	34-37	0/2/0	North Carolina
<i>P. triseriata</i>	22	22-29	0/3/19	Virginia

Taxon	N	Size Range	Sex	Locality
Leptodactylidae				
Eleutherodactylus				
<i>E. antillensis</i>	8	12-29	1/1/6	Puerto Rico, St. Croix
<i>E. brittoni</i>	8	14-16	0/3/5	Puerto Rico
<i>E. cochraeae</i>	5	17-20	0/2/3	Puerto Rico
<i>E. coqui</i>	7	15-36	1/2/4	Puerto Rico
<i>E. hedricki</i>	1	34	0/0/1	Puerto Rico
<i>E. lentus</i>	11	12-35	1/2/8	St. Croix
<i>E. locustus</i>	3	17-18	0/2/1	Puerto Rico
<i>E. martinicensis</i>	14	17-38	0/7/7	Guadeloupe
<i>E. planirostris</i>	25	13-23	3/13/9	Florida
<i>E. portoricensis</i>	3	19-32	0/1/2	Puerto Rico
<i>Leptodactylus albilabris</i>	1	33	0/0/1	Puerto Rico
Microhylidae				
<i>Cophixalus cryptotympanum</i> ¹ ..	17	19-35	0/8/9	Papua New Guinea: Morobe
<i>Gastrophryne carolinensis</i> ...	25	20-31	0/5/20	Florida, North Carolina, Virginia
<i>Pherohapsis menziesi</i>	6	28-30	0/0/6	PNG: Central
<i>Sphenophryne palmipes</i>	9	27-46	0/5/4	PNG: Morobe
Myobatrachidae				
<i>Lechriodus melanopyga</i>	26	41-51	2/9/15	PNG: Central
Pelobatidae				
<i>Scaphiopus couchi</i>	10	44-68	0/3/7	Sonora
<i>S. hammondi</i>	5	38-53	0/5/0	New Mexico, Utah
<i>S. holbrookii</i>	6	21-57	2/0/4	Maryland, North Carolina, Virginia
Pelodryadidae				
<i>Litoria angiana</i>	14	52-74	0/1/13	PNG: Morobe
<i>L. bicolor</i>	25	20-29	0/6/19	PNG: Central
<i>L. bicolor</i>	4	22-25	0/3/1	PNG: Western
<i>L. caerulea</i>	23	61-86	0/11/12	PNG: Central
<i>L. congenita</i>	25	30-37	0/8/17	PNG: Central
<i>L. impura</i>	24	38-51	1/4/19	PNG: Central
<i>L. infrafronata</i>	30	24-117	8/8/14	PNG: Central
<i>L. micromembrana</i>	30	24-31	0/10/20	PNG: Morobe
<i>L. nasuta</i>	21	40-58	0/10/11	PNG: Central
<i>L. nigropunctata</i>	19	25-30	0/2/17	PNG: Northern
<i>L. thesaurensis</i>	25	34-39	0/0/25	PNG: Central
<i>L. vocivincens</i>	25	23-27	0/0/25	PNG: Central
<i>Nyctimystes foricula</i>	2	35	0/0/2	PNG: Morobe
<i>N. sp (gray)</i>	2	88	0/0/2	PNG: Morobe
Ranidae				
<i>Platymantis papuensis</i>	25	27-57	0/3/22	PNG: Morobe, Northern
<i>Rana aurora</i>	3	77-90	0/3/0	Washington
<i>R. catesbeiana</i>	20	45-159	1/10/9	Maryland, Virginia
<i>R. clamitans</i>	37	31-88	3/21/13	Indiana, Maryland
<i>R. dalmatina</i>	5	46-67	0/1/4	France
<i>R. grisea</i>	25	17-109	1/5/19	PNG: Central
<i>R. grisea</i>	7	59-89	0/2/5	PNG: Morobe
<i>R. gryllio</i>	1	67	0/0/1	Florida
<i>R. palustris</i>	22	30-80	0/8/14	Maryland
<i>R. papua</i>	17	26-75	0/10/17	PNG: Central, Western
<i>R. sylvatica</i>	15	37-59	0/4/11	Maryland
<i>R. utricularia</i>	24	29-77	0/11/13	Florida, Georgia, North Carolina
<i>R. virgatipes</i>	17	34-55	0/3/14	New Jersey, North Carolina
<i>R. sp. (middors. stripe)</i>	25	21-60	1/9/15	PNG: Morobe

1. This sample may be a mix of two or three species.

TABLE B.—Jumping performance (absolute) (species listed in same order as in Table A; sample size same; values for mean and maximum jumping distances calculated from sums of mean and maximum distances of individual frogs; \bar{X} = mean; s = standard deviation)

Taxon	Mean jumping distance			Maximum jumping distance		
	\bar{X}	s	Range	\bar{X}	s	Range
A. truei.....	562.2	79.7	404-674	658.3	81.9	482-741
B. americanus.....	204.5	54.3	121-338	248.6	64.8	151-408
B. boreas.....	248.3	52.1	185-311	304.8	57.8	234-367
B. fowleri.....	248.9	89.0	133-401	303.4	114.1	154-499
B. marinus (FL).....	404.8	53.9	293-473	469.6	56.9	351-557
B. marinus (PNG).....	271.5	107.4	77-458	338.7	140.6	87-535
B. microscaphus.....	242.5	20.9	225-292	293.8	25.3	257-335
B. punctatus.....	187.0	30.6	123-215	222.4	43.0	140-280
B. quercicus.....	73.1	7.7	58-85	85.6	7.5	71-101
B. terrestris.....	209.6	34.6	130-264	249.5	45.6	149-333
C. inquinalis.....	338.1	35.0	282-402	434.0	42.7	339-491
C. nubicola.....	213.2	29.5	150-279	269.6	49.2	189-356
C. sp.....	243.0	64.5	147-338	286.7	80.4	162-395
C. pratti.....	244.1	47.7	168-300	326.8	55.2	244-376
C. trinitatis.....	364.2	-	324-410	394.2	-	356-455
D. auratus.....	164.8	37.4	77-228	244.3	49.3	113-311
D. minutus.....	118.1	23.2	81-158	171.8	32.5	113-209
D. pictus.....	455.9	-	380-531	554.0	-	464-644
A. crepitans.....	429.4	99.6	232-683	551.2	106.1	345-837
A. gryllus.....	474.4	151.7	170-1000	628.1	180.8	260-1277
H. andersoni.....	407.0	-	342-473	494.0	-	438-550
H. arenicolor.....	419.2	-	312-498	487.3	-	403-505
H. chrysoscelis.....	446.1	152.8	199-609	503.0	155.9	255-692
H. cinerea.....	496.8	79.5	354-657	565.2	85.2	396-718
H. crucifer.....	504.9	85.4	284-692	606.6	84.5	468-814
H. femoralis.....	394.7	83.6	196-561	484.6	91.4	231-639
H. gratiosa.....	470.2	-	422-518	514.0	-	472-645
H. regilla.....	465.8	70.3	309-590	536.6	72.9	342-645
H. squirella.....	565.5	56.9	363-641	636.6	70.1	446-757
H. versicolor.....	464.1	98.2	236-646	517.6	114.5	248-763
L. ocularis.....	348.6	72.8	232-471	427.5	81.1	257-563
O. septentrionalis.....	807.5	158.9	504-1087	910.5	171.1	535-1200
P. brachyphona.....	674.7	-	-	75.1	-	-
P. brimleyi.....	435.2	38.2	362-501	488.9	53.2	411-582
P. nigrita l.....	264.9	58.6	207-353	354.4	63.1	251-439
P. ornata l.....	291.1	-	234-347	345.0	-	293-397
P. triseriata.....	442.9	64.8	275-528	498.6	78.6	305-583
E. antiellensis.....	213.2	57.6	137-316	267.5	56.6	194-379
E. brittoni.....	226.2	43.5	171-290	299.4	77.3	204-431
E. cochranæ.....	129.9	23.1	108-169	185.0	21.3	177-202
E. coqui.....	291.0	115.6	124-428	386.6	152.2	130-575
E. hedricki.....	290.6	-	-	359.0	-	-
E. lentus.....	346.6	140.6	185-692	391.4	145.2	225-743
E. locustus.....	194.4	-	152-230	258.7	-	176-324
E. martinicensis.....	240.9	53.1	170-344	287.7	72.7	183-430
E. planirostris.....	238.1	60.6	162-371	281.2	70.8	190-424
E. portoricensis.....	257.5	-	181-392	316.0	-	209-457
L. albilabris.....	410.3	-	-	454.0	-	-
C. cryptotympanum 2 ...	382.6	82.9	264-470	472.1	94.0	332-666
G. carolinensis.....	190.6	35.8	115-258	224.4	38.2	143-311
P. menziesi.....	183.9	28.8	156-233	291.2	53.3	243-395
S. palmipes.....	537.1	80.5	386-605	617.2	103.3	459-781
L. melanopyga.....	938.5	136.8	620-1172	1041.8	164.3	731-1430
S. couchi.....	227.7	22.9	192-278	260.0	28.8	213-311
S. hammondi.....	252.2	20.5	219-271	300.2	37.3	239-335
S. holbrookii.....	187.5	22.4	153-213	224.2	38.6	179-281
L. angiana.....	826.2	126.4	586-1063	877.6	136.9	623-1130

Taxon	Mean jumping distance			Maximum jumping distance		
	\bar{X}	s	Range	\bar{X}	s	Range
L. bicolor (C).....	567.3	127.7	280-799	622.9	122.9	327-837
L. bicolor (W).....	486.2	-	450-515	511.0	-	479-546
L. caerulea.....	564.9	56.8	428-644	610.7	60.8	465-695
L. cogenita.....	679.7	82.2	546-846	741.6	89.4	602-910
L. impura.....	1044.1	79.1	984-1432	1151.9	103.3	871-1190
L. infrafnata.....	852.4	387.3	199-1370	978.9	460.4	226-1771
L. micromembrana.....	530.0	74.2	315-644	575.2	91.8	315-726
L. nasuta.....	1216.3	235.8	923-1908	1381.8	294.7	957-2267
L. nigropunctata.....	509.3	68.2	414-613	566.9	90.4	432-713
L. thesaurensis.....	843.1	75.4	707-1040	902.1	84.5	743-1079
L. vocivincens.....	632.1	84.6	452-782	691.6	100.5	496-882
N. foricula.....	795.5	-	767-824	856.5	-	842-871
N. sp.....	938.5	-	938-939	1160.0	-	1050-1270
P. papuensis.....	806.1	136.4	461-1057	900.0	129.5	585-1143
R. aurora.....	715.3	-	518-841	872.7	-	750-943
R. catesbeiana.....	708.0	195.4	373-1072	865.6	247.3	449-1295
R. clamitans.....	613.7	159.2	373-934	726.4	188.9	420-1180
R. dalmatina.....	470.5	83.0	361-586	676.6	186.7	555-1000
R. grisea (C).....	1015.7	400.6	233-1591	1137.4	452.4	253-1811
R. grisea (M).....	1086.8	194.3	816-1345	1212.9	241.5	845-1619
R. grylio.....	507.6	-	-	568.0	-	-
R. palustris.....	656.4	136.9	306-885	757.6	163.4	376-1018
R. papua.....	837.8	339.7	356-1492	920.2	351.9	432-1539
R. sylvatica.....	653.0	124.4	494-839	745.0	162.2	541-992
R. utricularia.....	714.8	171.1	399-1035	896.6	222.6	455-1255
R. virgatipes.....	328.6	49.3	233-416	408.0	57.4	286-518
R. sp.....	974.3	195.6	356-1174	1055.2	208.8	397-1369

- 1 Held overly long in captivity prior to testing; jumps may not be truly representative.
- 2 Although very similar in appearance and collected along the same mountain stream, the sample may be a mix of two or three species.

TABLE C.—Jumping performance (relative) (calculated by dividing mean and maximum jumping distance of each frog by that frog's snout-vent length; resulting value = number of body lengths in jump of each frog; abbreviations same as Table B)

Taxon	Mean jumping ability			Maximum jumping ability		
	\bar{X}	s	Range	\bar{X}	s	Range
A. truei.....	14.6	1.0	13.4-16.2	17.1	1.1	15.3-18.6
B. americanus.....	3.9	0.9	2.3-6.0	4.7	0.9	3.1-6.8
B. boreas.....	3.1	0.2	2.9-3.5	3.9	0.4	3.6-4.4
B. fowleri.....	5.2	1.5	2.6-8.3	6.4	1.8	3.0-10.8
B. marinus (FL).....	4.4	0.6	3.3-6.0	5.0	0.6	4.0-6.6
B. marinus (PNG).....	4.6	1.3	2.5-7.0	5.6	1.5	3.1-8.4
B. microscaphus.....	4.3	0.6	3.5-5.2	5.2	0.9	3.9-6.5
B. punctatus.....	4.3	0.8	2.7-5.2	5.0	0.9	3.1-6.2
B. quercicus.....	3.3	0.4	2.5-3.9	3.8	0.4	3.0-4.6
B. terrestris.....	4.5	0.8	2.9-6.3	5.3	1.1	3.6-8.0
C. inqualis.....	14.2	1.6	11.8-16.8	18.3	1.5	15.1-20.0
C. nubicola.....	14.6	1.9	10.7-17.6	18.5	3.5	11.8-24.5
C. sp.....	12.4	2.8	8.4-16.1	14.6	3.7	10.1-20.8
C. pratti.....	13.3	0.8	12.3-14.2	18.0	1.8	15.7-20.3
C. trinitatis.....	16.1	-	13.9-18.6	17.4	-	14.5-19.9
D. auratus.....	6.5	1.1	4.3-8.6	9.7	2.0	6.2-13.8
D. minutus.....	8.8	1.4	7.3-10.7	12.8	1.9	10.0-15.4
D. pictus.....	7.5	-	6.8-8.2	9.1	-	8.3-9.9
A. crepitans.....	21.9	3.6	14.5-27.8	28.2	3.9	20.3-38.0
A. gryllus.....	23.4	6.6	13.3-48.3	31.1	8.4	20.1-61.7
H. andersoni.....	11.7	-	10.7-12.6	14.2	-	13.7-14.7
H. arenicolor.....	9.8	-	7.0-11.4	11.3	-	9.1-12.9
H. chrysoscelis.....	11.4	3.2	6.7-15.2	13.0	3.2	7.5-17.0
H. cinerea.....	13.2	2.0	9.7-17.1	15.0	2.0	11.1-20.0
H. crucifer.....	19.1	3.2	11.0-25.5	22.9	3.0	17.8-29.9
H. femoralis.....	13.6	2.2	9.9-18.7	16.8	2.8	12.4-21.9
H. gratiosa.....	9.4	-	8.4-10.4	10.3	-	9.4-11.1
H. regilla.....	13.8	2.3	8.9-17.6	15.8	2.2	9.8-19.2
H. squirella.....	17.6	1.6	13.4-20.3	19.8	2.0	16.2-23.0
H. versicolor.....	10.6	2.1	6.9-14.2	11.8	2.3	7.6-16.5
L. ocularis.....	23.9	3.4	18.5-30.7	29.4	4.5	22.0-36.9
O. septentrionalis.....	13.5	2.9	8.1-18.8	15.2	3.2	9.3-20.2
P. brachyphona.....	24.7	-	-	27.5	-	-
P. brimleyi.....	15.4	1.9	11.8-18.7	17.2	2.5	13.5-21.3
P. nigrita 1.....	10.6	2.1	8.5-14.2	14.2	2.3	10.2-17.3
P. ornata 1.....	8.4	-	6.4-10.4	9.9	-	8.0-11.8
P. triseriata.....	16.8	2.2	12.3-20.4	18.9	2.7	13.5-22.6
E. antillensis.....	10.6	2.3	7.6-15.5	13.5	2.6	10.7-19.4
E. brittoni.....	15.0	3.4	11.2-19.3	19.9	5.7	13.3-28.9
E. cochranæ.....	7.1	1.1	6.2-8.9	10.2	1.6	7.5-11.8
E. coqui.....	11.1	2.0	8.0-13.5	14.9	3.8	8.4-21.1
E. hedricki.....	8.6	-	-	10.6	-	-
E. lentus.....	15.4	3.1	8.8-19.7	17.6	3.6	9.8-22.1
E. locustus.....	10.9	-	8.4-12.9	14.5	-	9.7-18.2
E. martinicensis.....	9.4	2.9	5.2-18.3	11.1	3.7	6.2-22.3
E. planirostris.....	14.2	2.3	10.3-18.7	16.7	2.5	11.7-21.0
E. portoricensis.....	10.6	-	9.1-12.1	13.3	-	10.6-15.2
L. albilabris.....	12.5	-	-	13.8	-	-
C. cryptotypanum 2 ..	15.0	4.0	8.3-23.6	18.4	4.2	10.5-24.9
G. carolinensis.....	7.2	1.4	4.3-10.3	8.4	1.7	5.3-12.6
P. menziesi.....	6.5	1.1	5.7-8.3	10.3	2.0	8.5-14.3
S. palmipes.....	13.8	1.0	12.2-15.3	15.8	1.2	13.6-17.1
L. melanopyga.....	20.4	3.1	13.5-25.7	22.7	3.6	15.9-28.1
S. couchi.....	4.2	0.5	3.4-4.8	4.8	0.8	3.5-6.3
S. hammondi.....	5.3	0.8	4.7-6.6	6.3	0.9	5.1-7.6
S. holbrookii.....	5.5	1.5	3.1-7.1	6.4	1.5	4.2-8.3
L. angiana.....	14.8	2.9	9.6-20.2	15.7	3.0	10.8-21.0

Taxon	Mean jumping ability			Maximum jumping ability		
	\bar{X}	s	Range	\bar{X}	s	Range
L. bicolor (C).....	24.4	5.3	11.5-32.6	26.8	5.0	14.8-34.2
L. bicolor (W).....	20.4	-	19.1-21.5	21.4	-	19.5-22.6
L. caerulea.....	7.8	1.1	6.0-9.5	8.4	1.2	6.6-10.8
L. congenita.....	20.0	2.6	15.5-24.3	21.8	2.7	20.0-26.7
L. impura.....	22.8	2.1	18.3-27.9	25.1	2.4	21.3-30.4
L. infrafrenata.....	13.4	3.1	8.1-19.3	15.8	3.5	8.9-22.4
L. micromembrana.....	19.4	3.3	10.3-25.5	21.0	4.0	10.3-28.7
L. nasuta.....	25.4	5.7	17.4-43.3	29.0	7.0	18.1-51.4
L. nigropunctata.....	18.7	2.7	15.3-24.5	20.8	3.5	15.7-28.5
L. thesaurensis.....	22.9	1.8	19.2-26.5	24.5	2.0	20.2-36.0
L. vocivincens.....	25.6	3.7	18.5-31.9	28.0	4.4	19.6-36.0
N. foricula.....	22.6	-	21.9-23.3	24.4	-	24.1-24.7
N. sp.....	10.7	-	-	13.2	-	11.9-14.4
P. papuensis.....	19.6	2.9	13.1-23.9	22.0	3.1	14.6-27.3
R. aurora.....	8.7	-	5.7-10.9	10.6	-	8.3-12.3
R. catesbeiana.....	7.7	2.3	4.6-12.3	9.3	2.4	5.9-13.3
R. clamitans.....	10.8	1.6	6.8-14.0	12.7	2.0	9.1-16.8
R. dalmatina.....	9.5	2.3	6.6-12.2	13.7	4.5	8.6-20.9
R. grisea (C).....	17.1	2.7	12.0-22.4	19.2	3.5	12.6-25.5
R. grisea (M).....	15.0	2.4	10.5-16.3	16.9	3.3	10.9-21.1
R. gryllo.....	7.6	-	-	8.5	-	-
R. palustris.....	11.5	2.1	6.6-16.4	13.3	2.5	8.0-19.2
R. papua.....	16.8	1.9	12.7-19.8	18.6	1.8	14.9-21.6
R. sylvatica.....	14.2	2.6	9.1-17.5	16.1	3.3	10.2-21.0
R. utricularia.....	12.2	3.0	7.8-18.6	15.2	3.5	8.7-23.2
R. virgatipes.....	7.0	1.0	5.8-8.8	8.7	1.1	7.3-10.8
R. sp.....	18.6	1.5	14.9-21.2	20.2	1.4	16.4-23.4

- 1 Jumps may not be representative, overly long in captivity.
- 2 Sample may be composed of two or three species.

TABLE D.—Body dimensions (least square regression equation, $Y=A+BX$, and its linear correlation coefficient, r , presented only for samples of 8 or more individuals; Y = cube root of body weight in grams, X = snout-vent length in centimeters, "length" and "weight" = estimated means for adult males, Z = length derived from jump test group, USNM = length derived from jump test group and alcoholic specimens in the Smithsonian collection; weights of amphibians are seldom listed in literature, so all weights are derived from regression equation when $r \geq 0.85$, otherwise from weight of similarly sized individual in sample; FL = Florida; PNG = Papua New Guinea; W = Western District, PNG; C = Central District, PNG; M = Morobe District, PNG)

Taxon	A	B	r	Length	Weight	Source
A. truei.....	0.243	0.374	0.97	4.0	5.3	Metter, 1964
B. americanus.....	-0.206	0.524	0.99	6.4	31.2	Z
B. boreas.....	-	-	-	7.5	50.2	Karlstrom, 1962
B. fowleri.....	-0.102	0.510	0.99	5.4	18.7	Minton, 1972
B. marinus (FL).....	0.150	0.437	0.99	10.1	94.9	Z
B. marinus (PNG).....	-0.155	0.492	0.99	8.0	60.2	Zug <i>et al.</i> , 1975
B. microscephus.....	-0.397	0.567	0.97	5.8	24.2	Blair, 1955
B. punctatus.....	-0.107	0.465	0.98	4.5	7.8	Storer, 1925
B. quercicus.....	-0.065	0.510	0.90	2.2	1.2	Z
B. terrestris.....	-0.317	0.529	0.93	5.9	22.0	Duellman & Schwartz, 1958
C. inguinalis.....	0.206	0.398	0.94	2.5	1.7	Edwards, 1974
C. nubicola.....	0.286	0.328	0.89	1.6	0.5	Edwards, 1974
C. sp.....	-	-	-	2.0	1.0	Z
C. pratti.....	-	-	-	1.9	0.9	Edwards, 1974
C. trinitatis.....	-	-	-	2.0	0.9	Z
D. auratus.....	0.056	0.446	0.98	3.1	3.0	Silverstone, 1975
D. minutus.....	0.156	0.415	0.87	1.3	0.3	Silverstone, 1975
D. pictus.....	-	-	-	5.6	-	Knoepffler, 1961
A. crepitans.....	0.103	0.406	0.96	2.0	0.8	Z
A. gryllus.....	0.014	0.452	0.97	2.1	0.9	Z
H. andersoni.....	-	-	-	3.7	4.0	Noble & Noble, 1923
H. arenicolor.....	-	-	-	4.3	5.6	Z
H. chrysoscelis.....	0.002	0.425	0.93	3.9	4.6	Z
H. cinerea.....	0.236	0.322	0.94	4.6	5.1	Duel. & Schw., 1958
H. crucifer.....	0.081	0.389	0.71	2.6	1.3	Z
H. femoralis.....	0.019	0.406	0.98	2.9	1.8	Z
H. gratiosa.....	-	-	-	6.1	-	Duel. & Schw., 1958
H. regilla.....	0.112	0.391	0.89	3.5	3.2	Jameson <i>et al.</i> , 1966
H. squirella.....	0.320	0.321	0.83	3.2	2.5	Z
H. versicolor.....	0.251	0.362	0.80	4.4	6.2	Z
L. ocularis.....	0.065	0.358	0.98	1.4	0.2	Duel. & Schw., 1958
O. septentrionalis....	-0.298	0.454	0.98	5.7	12.0	Duel. & Schw., 1958
P. brachyphona.....	-	-	-	2.8	-	Walker, 1932
P. brimleyi.....	-0.297	0.535	0.95	2.8	1.7	Z
P. nigrita.....	-0.579	0.633	0.80	2.5	1.0	Z
P. ornata.....	-	-	-	3.1	-	Harper, 1937
P. triseriata.....	-0.046	0.452	0.86	2.6	1.4	Z
E. antillensis.....	0.025	0.416	0.99	2.5	1.2	USNM
E. brittoni.....	0.099	0.393	0.95	1.5	0.3	Z
E. cochraeae.....	-	-	-	1.7	0.3	USNM
E. coqui.....	-	-	-	3.7	3.6	Thomas, 1966
E. hedricki.....	-	-	-	3.4	-	Z
E. lentus.....	0.029	0.409	0.99	2.5	1.2	Z
E. locustus.....	-	-	-	1.8	0.4	USNM
E. martinicensis.....	0.013	0.422	0.99	2.4	1.1	Z
E. planirostris.....	0.045	0.417	0.96	1.6	0.3	Z
E. portoricensis.....	-	-	-	2.9	-	USNM
L. albilabris.....	-	-	-	3.5	-	Heyer, pers. comm.
C. cryptotypanum ¹	0.116	0.426	0.99	2.4	1.5	Z
G. carolinensis.....	0.140	0.420	0.90	2.8	2.3	Z
P. menziesi.....	-	-	-	2.8	2.2	Z
S. palmipes.....	0.031	0.490	0.99	3.4	4.9	Z

Taxon	A	B	r	Length	Weight	Source
L. melanopyga.....	0.108	0.432	0.94	4.5	8.6	Z
S. couchi.....	0.067	0.467	0.99	5.8	20.9	Z
S. hammondi.....	-	-	-	5.2	14.2	Storer, 1925
S. holbrooki.....	-	-	-	4.9	10.6	Minton, 1972
L. angiana.....	0.007	0.391	0.97	5.5	10.0	Z
L. bicolor (C).....	-0.105	0.450	0.95	2.3	0.8	Z
L. bicolor (W).....	-	-	-	2.2	0.7	Z
L. caerulea.....	0.108	0.396	0.91	7.1	24.9	Z
L. congenita.....	0.284	0.324	0.63	3.4	2.7	Z
L. impura.....	-0.073	0.422	0.86	4.6	6.5	Z
L. infrafronata.....	-0.029	0.425	0.99	8.3	42.8	Z
L. micromembrana.....	-0.008	0.426	0.93	2.6	1.3	Z
L. nasuta.....	-0.482	0.551	0.96	4.4	7.3	Z
L. nigropunctata.....	-0.014	0.384	0.77	2.7	1.1	Z
L. thesaurensis.....	0.645	0.210	0.74	3.7	2.9	Z
L. vocivincens.....	0.240	0.306	0.64	2.5	1.0	Z
P. papuensis.....	0.256	0.380	0.97	4.1	6.0	Z
R. aurora.....	-	-	-	5.4	17.5	Storer, 1925
R. catesbeiana.....	-0.092	0.479	0.99	12.0	180.9	Minton, 1972
R. clamitans.....	-0.018	0.463	0.99	7.2	36.4	Minton, 1972
R. dalmatina.....	-	-	-	4.7	8.6	Z
R. grisea (C).....	-0.078	0.462	0.99	7.4	37.3	Z
R. grisea (M).....	-	-	-	6.7	22.0	Z
R. gryllo.....	-	-	-	10.6	-	Duel. & Schw., 1958
R. palustris.....	0.044	0.438	0.96	5.4	13.8	Z
R. papua.....	-0.113	0.446	0.99	6.6	22.7	Z
R. sylvatica.....	0.143	0.425	0.89	4.4	8.2	Z
R. utricularia.....	-0.080	0.466	0.98	5.6	16.3	Z
R. virgatipes.....	-0.095	0.472	0.97	4.7	9.6	Z
R. sp.....	0.536	0.324	0.96	5.7	13.5	Z

1. Sample may be composed of two or three species.

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