# Anuran Locomotion—Structure and Function: The Jumping Forces of Frogs

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The flight of a jumping frog has been frequently compared to the trajectory of a missile or projectile (Gray, 1953; Gans and Rosenberg, 1966; Calow and Alexander, 1973). As such, the general ballistic equation and its related equations with minor modifications have been accepted as adequate mathematical descriptors of a frog's jump. To date, these equations have been examined only by using a single value of terminal velocity at liftoff or distance jumped (Gray, 1968; Calow and Alexander, 1973). Our goal has been to record the maximum force at liftoff in a variety of frog species in order to determine if our measure of force and the general ballistic equation or a modification thereof provide a reasonable estimate of terminal velocity and distance jumped.

## Materials and Methods

Adult males of 10 species of frogs (scientific names and sample sizes listed in Table 1) were collected in Oktibbeha and Hancock Counties, Mississippi, during the spring of 1975. The weight (nearest 0.1 g), snout-vent length, and right hindlimb length (nearest 0.1 mm) were recorded for each frog immediately following its jumping test. In most cases, the frogs were tested within 24 hr of capture.

The force platform was a water-filled tambor constructed from a plastic funnel (64 mm mouth diameter) covered by a thin plastic diaphragm. The tambor was connected via Tygon tubing through a Strathmore pressure transducer to a Beckman Dynagraph. The tambor was calibrated by placing metal balance weights on the diaphragm. The resulting Dynagraph records provide a summation of the forces applied during jumping and the duration of these forces.

For the tests, the tambor diaphragm was covered with moist absorbent paper in order to provide sufficient friction to enable the frog to jump normally. The frog was placed on the diaphragm with its hindfeet in the center, thus permitting maximum downward displacement of the diaphragm. Each frog was tested once.

## Results and Discussion

The initial data are summarized in Table 1. Since the samples were restricted to adult males, variations in the length measurements of each species are low (coefficients of variation, 5–8). In contrast, weight variation is higher (cv, 10–35), and the force and its duration are even higher (cv, 15–50 and 20–85, respectively). A portion of variation in the latter 2 parameters undoubtedly results from the design of the force platform and experimental procedure; however, consecutive leaps of a frog are seldom equidistant (Zug, 1978). Thus, the jumping distances of a single frog or a sample of equal-sized frogs will show considerable variation as will also the force and duration that are responsible for propelling the frog forward.

The naturalness of the force data may be evaluated by using these data to estimate the terminal velocities prior to liftoff and the distances traveled (Table 2). In most cases, these estimates differ only slightly from actual jumping distances, i.e., distances from Zug (1978). The estimated velocities and distances, hence the forces, are lower than "normal" for *Hyla chrysoscelis*, *H. gratiosa*, and *Pseudacris triseriata*. Presumably, the individuals of these species were not jumping normally, because the similarity of actual

Table 1.—A summary of the jumping tests. The first number in each column is the mean, the second the standard deviation.

| | N | Snout-vent length (mm) | Hindlimb length (mm) | Body weight (g) | Force (g) | Duration of force (sec) |
|---|---|---|---|---|---|---|
| **Hylidae** | | | | | | |
| Acris gryllus | 4 | 21.5 ± 1.7 | 40.6 ± 1.3 | 1.0 ± .32 | 6.3 ± 2.7 | .054 ± .047 |
| Hyla avivoca | 23 | 34.8 ± 2.1 | 53.3 ± 3.5 | 2.5 ± .54 | 11.4 ± 3.0 | .030 ± .017 |
| H. chrysoscelis | 5 | 44.2 ± 3.0 | 61.2 ± 4.9 | 6.4 ± 1.4 | 12.9 ± 3.0 | .027 ± .011 |
| H. cinerea | 8 | 55.6 ± 2.8 | 86.3 ± 5.8 | 9.2 ± 1.2 | 23.3 ± 7.4 | .058 ± .034 |
| H. crucifer | 3 | 30.8 ± 1.4 | 47.0 ± 5.1 | 1.8 ± .15 | 9.1 ± 1.4 | .035 ± .008 |
| H. femoralis | 3 | 32.4 ± 0.8 | 47.4 ± 2.0 | 2.2 ± .60 | 8.4 ± 4.2 | .042 ± .013 |
| H. gratiosa | 3 | 63.2 ± 4.0 | 91.1 ± 3.3 | 11.4 ± 4.2 | 22.2 ± 1.4 | .066 ± .034 |
| Pseudacris nigrita | 1 | 28.0 | 41.1 | 1.0 | 3.2 | .027 |
| P. triseriata | 1 | 31.7 | 45.0 | 1.8 | 2.8 | .037 |
| **Microhylidae** | | | | | | |
| Gastrophryne carolinensis | 1 | 29.5 | 33.1 | 2.1 | 6.0 | 0.047 |

Table 2.—A comparison of estimated jumping distances to actual jumping distances (from Appendix, Table B in Zug, 1978).[a]

| Taxon | Estimated Velocity (cm/sec) | Estimated Distance (cm) | Mean Distance | Difference |
|---|---|---|---|---|
| A. gryllus | 223.9 | 51.2 | 47.4 | 3.8 |
| H. avivoca | 218.3 | 48.6 | | |
| H. chrysoscelis | 155.5 | 24.7 | 44.6 | −19.9 |
| H. cinerea | 207.0 | 43.7 | 49.7 | −6.0 |
| H. crucifer | 215.8 | 47.5 | 50.5 | −3.0 |
| H. femoralis | 187.5 | 35.9 | 39.5 | −3.6 |
| H. gratiosa | 186.5 | 35.5 | 47.0 | −11.5 |
| P. nigrita | 160.6 | 26.3 | 26.5 | −0.2 |
| P. triseriata | 117.1 | 14.0 | 44.3 | −30.3 |
| G. carolinensis | 136.2 | 18.9 | 19.1 | −0.2 |

[a] Velocities were calculated from Gray's (1968) force equation $F = (WV^2) \div (2\,g\,s)$; W, body weight; g, gravity; s, hindlimb length. The estimated distances were calculated from the ballistic equation (Gans and Rosenberg, 1966), $D = (V^2 \sin 2\theta) \div g$; the angle was assumed to be 45°. Note that a deviation from 45° will decrease jumping distance but not significantly so until about ±10°.

and estimated distances for the other species indicate that the force platform and experimental procedure were providing an accurate measure of the forces applied during natural jumping.

We must emphasize that the close similarity between the estimated and observed jumping distances derives only from Gray's and Gans' equations (see legend of Table 2). The equations $V = s \div t$ and $D = V^2 \div g$ (where V is average velocity during propulsive phase of jump; s, distance during propulsion or hindlimb length; t, time or duration of force; D, distance jumped) greatly underestimate velocity and jumping distance. An overestimate of velocity and jumping distance was obtained from the equations $A = Fg \div W$, $V = A \div t$, and $D = (V^2 \div g) \sin 2\theta$.

Table 3.—A linear correlation coefficient matrix comparing five jumping parameters in A. gryllus, H. cinerea, H. crucifer, H. femoralis, P. nigrita, and G. carolinensis.

| | BW | F | Du | Di | HL |
|---|---|---|---|---|---|
| Body weight | 1.00 | 0.96[a] | 0.55 | 0.22 | 0.93[a] |
| Force | | 1.00 | 0.43 | 0.47 | 0.94[a] |
| Duration | | | 1.00 | 0.10 | 0.37 |
| Distance (estim.) | | | | 1.00 | 0.35 |
| Hindlimb length | | | | | 1.00 |

[a] A significant correlation at 0.05 level.

An interspecific comparison of several jumping parameters (Table 3) shows significant positive correlations between force (Y) and body weight (X), force (Y) and hindlimb length (X), and body weight (Y) and hindlimb length (X). More force is required to propel a heavier frog; more force is produced by longer hindlimbs; and as a frog becomes larger, its body weight and hindlimb length increase. Although these correlations would be expected in an intraspecific comparison, they might not occur in an interspecific comparison, which includes frog species with different jumping behaviors and abilities. We suspect our results obtain from the preponderance of hylid species in the sample, because they are similar in behavior and ability. The low correlations between jumping distance and force or hindlimb length are surprising; force and hindlimb length are strongly correlated and are used to estimate the jumping distance, hence jumping distance would also be assumed to show a high correlation to both of them.

Gans and Rosenberg (1966) proposed that the force of a jump was proportional to 7/6 power of body weight in *Bufo marinus*. Although our data show a significant correlation between force and weight (Table 3: Y = 3.47 + 2.19X; Y

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$= 4.69X^{0.74}$, r $= 0.90$, Y, force; X, body weight), they are not suitable for testing this relationship, because bufonids are weak jumpers and our sample is dominated by strong jumpers. We do, however, wish to correct the typographical error in Gans' and Rosenberg's derivation, because $F^2M^{-2} \sim M^{1/3}$ becomes $F^2 \sim M^{7/6}$ or $F \sim M^{7/12}$ and not $F \sim M^{7/6}$.

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