

Allometric Relations of Take-off Speed and Power with Body Mass of Anuran Amphibians

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Previous studies have postulated that isometric animals exert similar locomotory capacity (speed, distance) because the amount of energy available for the motion would be the same regardless of body mass (m). To test propriety of this theory, we examined body shape and take-off potential of two frog species, *Rana nigromaculata* (powerful jumpers) and *Bombina orientalis* (slow hoppers). Morphological measurements included thigh muscle mass (indicative of total muscle force), hindlimb length (L , determining acceleration distance), and interlial width (shaping take-off motion). To gauge locomotory capacity, take-off speed (v) and take-off angle (θ) were measured from video analyses, and jump distance (R) and take-off power (P_i) were calculated from equations $R=v^2\sin^2\theta/g$ and $P_i=mv^3/2L$ (where g is the gravitational constant). Scaling exponents of morphometric variables for both species were 0.96-1.11 for thigh muscle mass, 0.28-0.29 for hindlimb length, and 0.30-0.36 for interlial width. Scaling exponents of locomotory performance for the two species were -0.01-0.14 for take-off speed, 0.24-0.31 for jump distance, and 0.66-0.84 for take-off power. The results demonstrate that the frogs of this study showed isometric body shape within species, but that take-off response changed allometrically with body mass, indicating that these data did not fully support the previous proposition. An exception was found in take-off speed of *B. orientalis*, in which the speed changed little with body mass (slope = -0.01). These findings suggest that the energy availability approach did not properly explain the apparent allometric relations of the take-off response in these animals and that an alternative model such as a power production approach may be worth addressing.

Scaling of the skeleto-muscular system offers an opportunity to comprehend how body size (mass or length) influences the locomotory capacity of animals of similar taxa (Gabriel, 1984). In isometric relations, smaller animals can be envisioned as miniatures of larger ones in terms of shape (Schmidt-Nielsen, 1984). Do they then function similarly too? A theory on take-off performance suggests that jump speed and distance may well be similar among isometric animals (Hill, 1950; Gabriel, 1984; Schmidt-Nielsen, 1984). Such a similar capacity, according to the theory, would be likely because a decrease in acceleration with body size is compensated by an increase in acceleration distance with size, and because metabolic energy per muscle mass required for take-off is essentially the same among these animals (Hill, 1950).

In anuran amphibians, previous morphometric studies on hindlimbs indeed showed isometric relations with body mass (hindlimb length a $\text{mass}^{0.33}$; Miller et al.,

1993; Choi and Park, 1996). However, locomotory tests have revealed that jump distance of some anurans scaled with body mass to the power of 0.2-0.36, which disagreed with those predicted by the theory (Emerson, 1978; Miller et al., 1993). In the present study, we examined the issue of locomotory scaling using two local anuran species, *Rana nigromaculata* and *Bombina orientalis*. The ranids are powerful jumpers with a laterally slender body shape and the *Bombina* are slow hoppers with a dorso-ventrally flat body shape (Choi and Park, 1996). If the theory is correct, take-off capacity will change isometrically with body mass (take-off potential $\propto \text{mass}^{0.0}$) in these species despite remote differences in their morphology and locomotory style.

Materials and Methods

Subjects

Frogs of the two species were collected from ponds and streams in Wonju, Kangwon-do, Republic of Korea, between May and August 1997-1998. The frogs were kept in a cage (length \times width \times height = 1.0 m \times 0.7 m \times 0.7 m) set on a natural stream and fed on

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insects coming into the cage before jump experiments. Two to four frogs were carried separately in numbered flasks to our laboratory and were weighed before the following experiments.

Take-off experiments

Experimental apparatus and procedures followed those described in a previous study (Choi and Park, 1996). Briefly, individual frogs were induced to jump at one end of a jump track ($l \times w \times h = 1.5 \text{ m} \times 0.2 \text{ m} \times 0.8 \text{ m}$) by rapidly moving a dark pad down over them. Jumping motions were recorded with a Sharp Slimcam VL-L50U video camera at a shutter speed of 1/2000. Each recording covered a lateral view of about 0.8-1.5 jumps depending on the jump distance of frogs. At least five jumps were induced for each frog, with a rest period of about 30 min between jumps. Ambient temperatures were 22°-24°C during experiments. Recorded videotapes were analyzed frame by frame using a jog-shutter function of a Philips four-head VR557 VTR. Each frame image was frozen and captured by a WinX Perfect frame grabber and was scanned on a cursor-based 17" color monitor connected with an IBM compatible 586 PC. Take-off speed was determined in a series of two consecutive frames of the recording and was calculated from the distance the subject moved between the two frames multiplied by the framing rate (30 Hz). The highest speed from the five or more trials of each frog was chosen for the maximum take-off speed (v) for that animal. Take-off angle (θ) was obtained from a tangent of the vertical to the horizontal distances that the animal moved between two frames right before and at take-off. Jump distance (R) and take-off power (P_t) were calculated from equations $R = v^2 \sin 2\theta / g$ and $P_t = mv^3 / 2L$, where g is the gravitational constant, m the body mass, and L the hindlimb length (see below) (Hildebrand, 1988).

Morphological measures

Mass of thigh muscle was measured on an analytical balance to the nearest 0.0001 g, while non-muscle tissues (e.g. nerves, blood vessels) were removed as much as possible. Hindlimb length was determined by adding individual lengths of the femur, tibiofibularis and foot bone. The foot bone length was the distance between the posterior tip of the heel and the distal end of the first phalange of the fourth toe. Interlimb width was determined by measuring the distance between the two ilia at the level of the sacral vertebra. The length parameters were measured to the nearest 0.01 mm with a pair of digital calipers.

Data presentation

We considered body mass as the independent variable in all the scaling relationships examined. Least square linear regression analyses on \log_{10} transformed data

were used to find intercepts and slopes in the scaling equations (Schmidt-Nielsen, 1984). Geometric and locomotor similarities among frogs within species were examined by t -tests on differences between the observed regression slopes and predicted slopes of corresponding variables (i.e., 1.00 for mass variables, 0.33 for length variables, and 0.00 for locomotory variables). Interspecific differences in morphological and locomotory data were tested by analysis of covariance (ANCOVA) on untransformed data (Packard and Boardman, 1986). Statistical procedures were performed with SPSS/PC+ (SPSS Inc.) and significance was judged at $P=0.05$ unless otherwise noted.

Results and Discussion

Regressions of snout-vent length of the frogs examined were completely overlapped between the two species (ANCOVA, $F_{1,26}=0.39$, $P=0.538$), and indicated the isometric body shape as the observed slope combined from both specimens was 0.306 (t -test on the regression slope, $P>0.05$; Table 1 and Fig. 1). Scaling of the three morphological variables with body mass also followed isometry within species (t -test on regression slopes, $P>0.05$), like other anuran species (Rand and Rand, 1966; Emerson, 1978; Miller et al., 1993) the slopes were 0.956-1.114 for thigh muscle mass, 0.279-0.289 for hindlimb length, and 0.342-0.367 for interlimb width (Table 1 and Fig. 2).

Despite the isometric body shape, take-off capacity of these frogs changed allometrically with body mass in both species (Table 1 and Fig. 3). The ranids had scaling slopes of 0.135 for take-off speed, 0.272 for

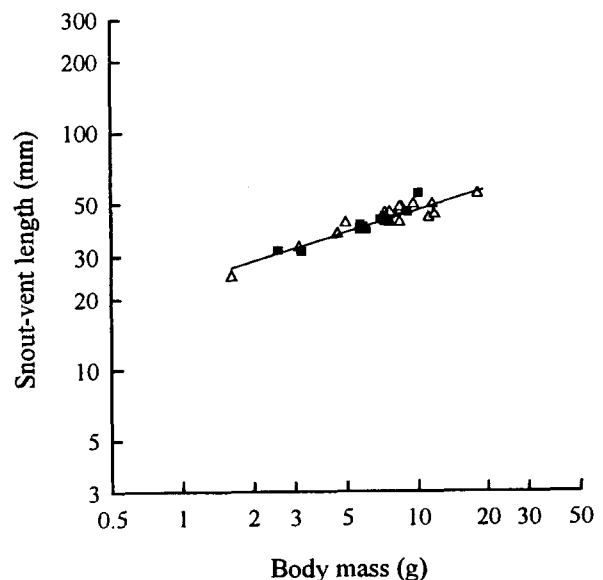


Fig. 1. Scaling of snout-vent length with body mass for *Rana nigromaculata* (Δ) and *Bombina orientalis* (\blacksquare). The regression line was fitted to data of both species combined, and regression slope and intercept for both species were given in Table 1.

Table 1. Scaling relations of morphological and locomotor variables with body mass in the two anuran species

Variable	n	Range	a [#]	b (95% CI*)	r ²	P [†]
<i>Rana nigromaculata</i>						
Body mass (g)	27	1.62 -34.20				
SVL (mm)**	16	24.76 -54.40	23.067	0.306 (0.254-0.429)	0.856	n.s.
Thigh muscle mass (g)	23	0.100- 3.595	0.062	1.114 (0.988-1.240)	0.941	n.s.
Hindlimb length (mm) ^a	16	35.91 -73.10	33.266	0.289 (0.246-0.332)	0.936	n.s.
Interlial width (mm) ^a	14	4.60 -10.70	3.689	0.342 (0.254-0.429)	0.856	n.s.
Take-off speed (m.s ⁻¹)	25	2.058- 3.555	1.854	0.135 (0.059-0.210)	0.372	n.s.
Jump distance (m)	24	0.421- 1.203	0.331	0.272 (0.105-0.439)	0.341	n.s.
Take-off power (W) ^a	14	0.525- 2.25	0.147	0.837 (0.493-1.276)	0.669	n.s.
<i>Bombina orientalis</i>						
Body mass (g)	24	2.25 - 10.12				
SVL (mm)**	13	31.26 - 55.05	23.067	0.306 (0.254-0.429)	0.856	n.s.
Thigh muscle mass (g)	22	0.117- 0.516	0.050	0.956 (0.692-1.221)	0.740	n.s.
Hindlimb length (mm) ^a	13	42.84 -59.75	31.622	0.279 (0.223-0.335)	0.916	n.s.
Interlial width (mm) ^a	13	6.59 -11.56	4.406	0.367 (0.216-0.518)	0.720	n.s.
Take-off speed (m.s ⁻¹)	12	1.508- 2.005	1.730	-0.01 (-0.12 -0.073)	0.014	sig.
Jump distance (m)	12	0.163- 0.331	0.182	0.167 (-0.06 -0.394)	0.211	n.s.
Take-off power (W) ^a	10	0.296- 0.589	0.090	0.660 (-0.911-2.500)	0.178	n.s.

The regression equation; Y=aM^b.

[#]The intercept is the antilog of the log₁₀ transformed data; *95% confidence interval; [†]Statistical significance determined at P=0.05; ^{**}Intercept (a) and exponent (b) are calculated from data of the two species combined. ^aA part of the data from 1997 were lost during the preparation of the specimen, which caused reduction of sample sizes in take-off power for both species.

jump distance, and 0.837 for take-off power; *Bombina* showed scaling slopes of -0.01 for speed, 0.167 for distance, and 0.660 for power. This indicated that the frogs of larger size within species jumped faster and farther, although the *Bombina* showed similar take-off speed along body mass. Scaling of jump distance in our frogs was fairly comparable with that of other anuran species (Rand and Rand, 1966; Zug, 1978; Miller et al., 1993). Zug (1978) reported that scaling slopes of jump distance ranged between 0.20 and 0.30 in more than 20 species of different jumping capacity, and that in only a few species did the slopes reach up to 0.4 or close to 0.0. To our knowledge, there are nearly no reports on the scaling of anuran take-off speed or power presently. Speeds of other locomotory modes such as swimming in fishes and sprint in lizards were found to increase with body mass, although in a few cases the speeds were independent of body mass (Beamish, 1978; Huey and Hertz, 1982; Garland, 1984).

The results of morphological and locomotory scaling of this study, together with those of other reports, lead us to consider the previous theory (energy availability model) to be hardly accepted. Although it would be true that energy per mass of the jumping muscle is constant regardless of body size (Schmidt-Nielsen, 1984), currently available information including this study demonstrate that energy output would not be the property featuring scaling of locomotory capacity, particularly in the fast jumping frogs. Bennet-Clark (1977) and Gabriel (1984) suggested that the major factor limiting such scaling patterns is the power (rate of energy release) rather than the quantity of energy *per se* for saltatory locomotion. According to Gabriel's model (1984), jump distance scales with mass to the power of 0.22, as given by her equation (No. 15). Although more practical examinations need to be made in her approach, the scaling value (0.22) supports well the locomotory scaling of the previous empirical studies (Bennet-Clark, 1977; Gabriel, 1984).

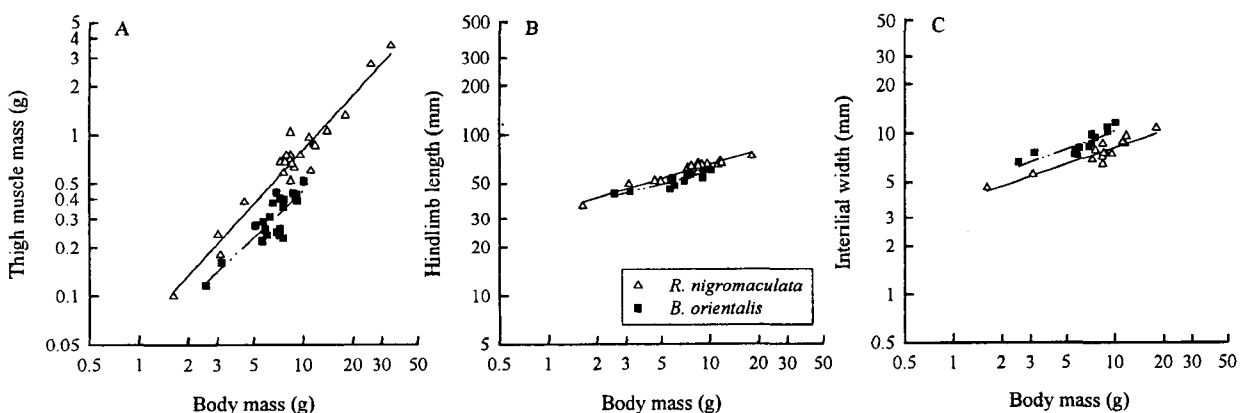


Fig. 2. Scaling of thigh muscle mass (A), hindlimb length (B), and interlial width (C) with body mass for the two frog species. Regression slopes and intercepts of the variables for both species were given in Table 1.

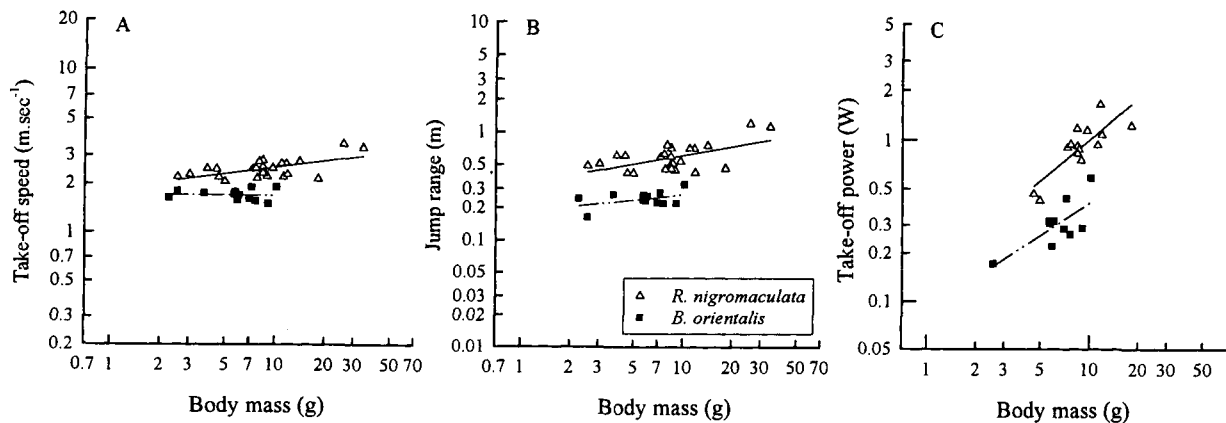


Fig. 3. Scaling of take-off speed (A), jump distance (B), and take-off power (C) with body mass for the two frog species. Regression slopes and intercepts of the variables for both species were given in Table 1.

and our own work.

An exception, however, apparently interferes with this interpretation for the speed data of the *Bombina* (Fig. 3A). In contrast to the allometric scaling of the take-off variables in the other species, take-off speed of the *Bombina* changed isometrically with body mass. One probable explanation may come from our sampling problem for the species. Scaling was performed over a mass range of only about a 4-fold difference in this species, which may not represent full scaling of its population. It was too difficult to collect froglets or very large frogs of this species in their habitat. In other anuran species (e.g. *Eleutherodactylus fitzingeri*, *Bufo typhonius*; I. Choi, unpublished data), froglets tend to exert significantly slower speed than larger ones of the same species, which results in the allometric scaling of the variable. Take-off performance of the frogs in that study was examined over a mass range of about 100-fold, and their body shape showed isometry within species. Another explanation may arise from an intrinsic metabolic capacity of the extensor muscles. Energy availability would be limited mainly by oxidative potential of the myofibers, but power production is more likely determined by glycolytic potential (Hochachka and Somero, 1984). This metabolic view may be relevant for our study animals, in that the glycolytic potential would be relatively more important for burst response of the ranids, while the oxidative potential for slow hopping in the *Bombina*. If this were true, the locomotory scaling of the *Bombina* would support the theory of energy output (Table 1 and Fig. 3). Enzymatic and histochemical studies on anuran muscles, however, have shown that fast-glycolytic fibers were dominant in fast frogs while fast-oxidative-glycolytic (not slow-oxidative) fibers were dominant in slow frogs (Mendiola et al., 1991; also see Choi and Park, 1996). The second explanation therefore needs further examination on the metabolic profiles of the hindlimb extensors for these animals (e.g. Ca^{2+} flux, concentrations of phosphagen; Hochachka and Somero, 1984).

In interspecific morphological comparisons (Fig. 2), *R. nigromaculata* had significantly greater thigh muscle mass and hindlimb length, and significantly smaller interilial width than *B. typhonius*, resulting in two separate regression lines for each variable (ANCOVA; $F_{1,42}=18.67$, $P<0.001$ for thigh muscle mass; $F_{1,26}=9.70$, $P<0.01$ for hindlimb length; $F_{1,24}=52.03$, $P<0.001$ for interilial width). Interspecific differences in the locomotory variables were also statistically significant, as were two separate regression lines seen in Fig. 3 (ANCOVA; $F_{1,43}=95.53$, $P<0.001$ for speed; $F_{1,33}=46.46$, $P<0.001$ for jump distance; $F_{1,19}=24.56$, $P<0.001$ for power). Thus, over the range of comparable size, *R. nigromaculata* were able to exert on average about 1.4-fold faster speed, 2.1-fold farther distance, and 1.7-fold greater power than the *Bombina*. These results suggest a typical trend in the relationship between form and function in locomotion. Animals of rapid, powerful motor function tend to have relatively long hindlimbs to confer a high-gear ratio, and a stream-lined body shape and massive muscles in the proximal limb segments to exert rapid movements of limbs and greater total force of muscles for take-off against gravity (Hildebrand, 1988; Choi and Park, 1996).

In conclusion, although some exception was noticed, take-off capacity of anurans in general scaled allometrically with body mass, and the scaling slopes were around 0.1 for speed, 0.2 for jump distance and 0.7 for power. Such scaling results seem to be hardly explained by the energy availability theory because the burst-type saltatory locomotion may be more likely limited by the power production potential of hindlimb muscles. This study would provide useful information on how the motor system of an animal is designed for the burst mode of locomotion or behavior.

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