RAPID COMMUNICATION

Morphometric Relationships of Take-Off Speed in Anuran Amphibians

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ABSTRACT   Locomotory speed correlates with muscle mass (determining force and stride rate), limb length (stride rate and distance), and laterally compressed body trunk (force and stride distance). To delineate generalization of the locomotory-morphometric relationships specifically in anuran amphibians, we investigated take-off speed and the three morphological variables from seven species, *Rana nigromaculata*, *R. rugosa*, and *Bombina orientalis*, *Eleuthrodectilus fitzingeri*, *E. diastema*, *Bufo typhonius*, *Colostethus flotator* and *Physalaemus pustulosus*. The fastest jumper *E. fitzingeri* (3.41 m s^{-1}) showed 2.49-fold greater speed than the slowest *B. typhonius*. Take-off speed correlated well with both thigh muscle mass relative to body mass and hindlimb length relative to snout-vent length (HL/SVL), but poorly correlated with the inter-ilial width relative to SVL. The best morphological predictor was HL/SVL (speed=−3.28+3.916 HL/SVL, r=0.968, $P < 0.0001$), suggesting that anuran take-off speed is portrayed well with high gear and acceleration distance characterized by hindlimbs. *J. Exp. Zool. 299A:99–102, 2003.* © 2003 Wiley-Liss, Inc.

INTRODUCTION

From mechanical perspectives, morphological components of the appendicular skeleto-muscular system comprise the major factors constraining animal locomotory speed (Hildebrand, '88; Duellman and Trueb, '96). Locomotory speed is defined by a product of stride distance times stride rate. Previous studies have shown that locomotory speed varies significantly within similar taxa, and that such variation paralleled morphological variation of the system (Emerson, '79; Gabriel, '84, Choi et al., 2000). Hildebrand ('88) summarized a number of examples on variation in locomotory speed, and depicted a trend of the locomotory-morphometric relationships: A fast animal lengthens stride distance by possessing relatively long limbs with favorable foot posture (e.g., unguligrade) and a laterally compressed body trunk that sets the vertically positioned pectoral girdle. The fast animal can also increase rate of stride by having high gear (a relatively longer out-lever arm versus an in-lever arm) in the limbs and by increasing contraction rate and power of a working muscle. Is this trend also applied to take-off speed in anuran amphibians?

Anurans show a significant variation in take-off capacity and body shape. Choi and Park ('96) examined take-off capacity of three anuran species, *Rana nigromaculata*, *R. rugosa*, and *Bombina orientalis*. They found that take-off speed of the two ranid species was 1.4 times that of the *Bombina* (2.4 versus 1.7 m.sec^{-1}). This difference seemed to partly reflect variation in several aforementioned morphological components in that the ranid species showed 1.2-fold greater hind limb length to body length, 2.0- to 2.5-fold greater thigh muscle mass relative to body mass, and 0.9-fold smaller inter-ilial width to body length than the *Bombina*. The present study extends the previous work of Choi and Park ('96), with more diverse species of anurans exhibiting wide interspecific variation in take-off performance. Our aim was to test generalization of the locomotory-morphometric relationship described by Hildebrand ('88) and to find a reasonable predictor for take-off speed in these leaping animals.

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MATERIALS AND METHODS

Subjects

Rana nigromaculata, *R. rugosa*, and *Bombina orientalis* were collected from rice fields and streams in Wonju, South Korea, between May and August 1998–2000. *Eleuthrodectilus fitzingeri*, *E. diastema*, *Bufo typhonius*, *Colostethus flotator* and *Physalaemus pustulosus* were collected along streams of forests in central Panama in February 1997 and March 1998. We used only male frogs, kept individually in numbered flasks, and measured body mass (M_b) to the nearest 0.0001 g after their bladder was emptied as in Choi et al., 2000.

Take-off experiments

All experiments were conducted between 17:00 and 22:00. Experimental procedures followed those in a previous study (Choi and Park, '96). Briefly, we induced individual frogs to jump at one end of a jump track ($l \times w \times h$=1.5 m $\times$ 0.2 m $\times$ 0.8 m) by rapidly moving a dark pad down behind them. We recorded jumping motions with a Samsung digital video camera SV-D100 at a shutter speed of 1/2000 sec. Each recording covered a lateral view of about 0.8–2.5 jumps depending on jump range of frogs. Five to seven jumps were induced for each frog, with a rest period of about 30 min between jumps. Recorded videotapes were analyzed frame by frame on a cursor-based 17'' PC monitor using a Philips VR557 and a WinX Perfect frame grabber. The anterior tip of the mouth was used to track movements of each frog. Peak take-off speed (v) 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 (60 Hz). Jump distance (D) is an important variable as well to gauge take-off capacity of anurans. However, because many of *E. fitzingeri* and *R. nigromaculata* jumped over the entire jump track, we approximated this variable using the equation, $D=v^2\sin2\theta/g$, where g is the gravitational constant and θ is the take-off angle (Hildebrand, '88). The jump distance calculated by this equation provides the level distance traveled by the center of mass between the time of take-off and the time it returns to the take-off height (Marsh and John-Alder, '94). Take-off angle was obtained from tangent of the vertical to the horizontal distances that the animal moved at the highest speed.

Morphological measure

The snout-vent length (SVL), hindlimb length (HL), and inter-ilial width (IW) were measured to the nearest 0.01 mm with a pair of digital calipers. HL was the length from the head of the femur to the distal end of the first phalange of the fourth toe. IW was the distance between two ilia at a level of the sacral vertebra. Thigh muscle mass (TM) was measured to the nearest 0.0001 g with an analytical balance after non-muscle tissues (e.g., nerves, blood vessels) were removed as much as possible.

Data presentation

All data were presented as mean ± 1 SD or otherwise noted. As previous studies revealed that anuran species show isometric body shape in general (Miller et al., '93; Choi et al., 2000), we normalized each of the morphological variables with body size, i.e., TM/M_b, HL/SVL, and IW/SVL. To determine relationships between morphological and locomotory variables, the first-order regression was obtained using the reduced major axis as in Clarke ('80) and Sokal and Rohlf ('98).

TABLE 1. *Descriptive statistics for morphological and locomotory variables for seven species examined[1]*

Species	n	M_b	SVL	TM/M_b	HL/SVL	IW/SVL	speed	distance	angle
E-fitzingeri	11	5.44+2.97	38.18+17.69	0.1019+0.0062	1.698+0.076	0.192+0.011	3.41+0.22	1.10+0.11	39.10+9.90
B. typhonius	7	4.71+3.81	36.66+11.41	0.0392+0.0061	1.144+0.043	0.273+0.016	1.37+0.17	0.17+0.05	34.57+9.29
P. pustulosus	12	1.74+0.27	27.74+1.50	0.0546+0.0050	1.302+0.047	0.228+0.011	1.72+0.29	0.27+0.10	32.77+8.62
C. flotator	6	0.32+0.02	15.99+0.30	0.0815+0.0066	1.305+0.035	0.193+0.009	1.70+0.27	0.27+0.10	32.58+7.16
R. nigromaculatoa	11	9.25+1.60	46.04+2.51	0.0757+0.0113	1.386+0.064	0.170+0.024	2.41+0.15	0.55+0.09	33.26+5.11
R. rugosa	10	9.72+6.21	43.03+9.18	0.0524+0.0089	1.454+0.059	0.178+0.022	2.19+0.29	0.44+0.12	32.86+7.49
B. orientalis	8	6.50+0.78	40.81+1.91	0.0388+0.0065	1.279+0.064	0.204+0.016	1.72+0.12	0.24+0.03	26.78+5.17

M_b: body mass (g); SVL: snout-vent length (mm); TM: thigh muscle mass (g); HL: hindlimb length (mm); IW: mter-ilial width (mm); speed: take-off speed (m s^{-1}); distance: jump distance (m); angle: take-off angle (°). Data are presented in mean ± 1 SD.
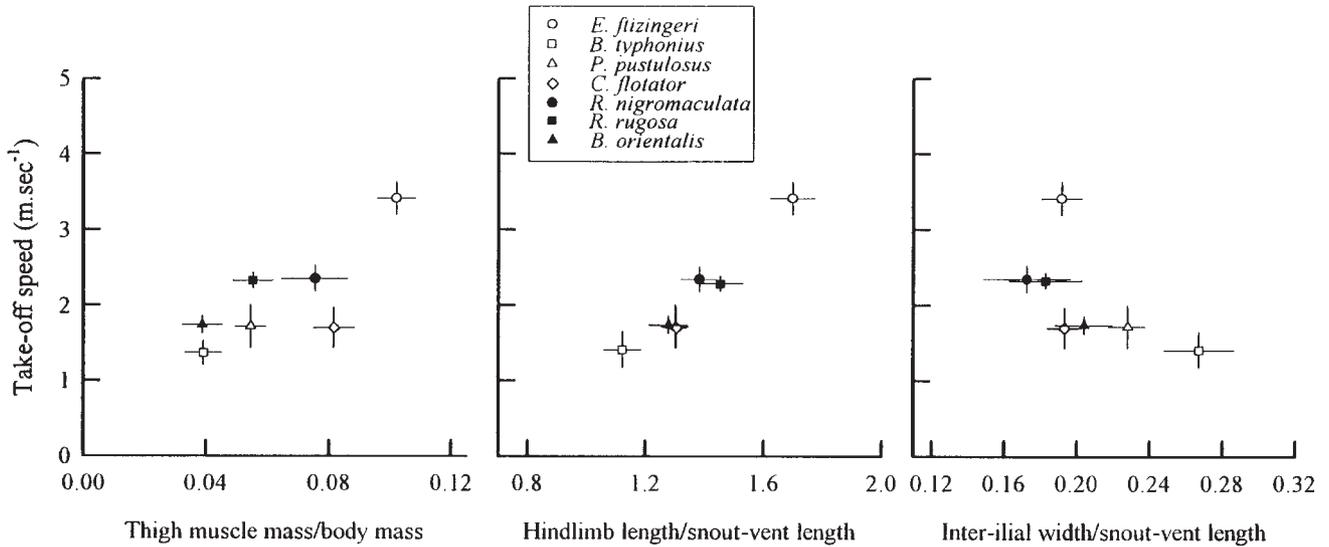
Fig. 1. Relationships of take-off speed with thigh muscle mass relative to body mass (TM/M_b), hindlimb length relative to snout-vent length (HL/SVL), and inter-ilial width relative to SVL in the seven anuran species. Among the three morpho- logical variables, take-off speed correlated well with TM/M_b and HL/SVL, with the latter the better predictor for the speed (take-off speed$=-3.28+3.916$ HL/SVL, r=0.968, $P < 0.0001$). Vertical and horizontal bars represent ± 1 SE of the mean.

RESULTS AND DISCUSSION

Descriptive statistics of morphological and loco-motory variables for the seven anuran species were summarized in Table 1. Figure 1 illustrates relationship of take-off speed to the three morphological variables (TM/M_b, HL/SVL, and IW/SVL). Table 2 summarizes regression and correlation analyses for the locomotory-morpho-logical relationships (including jump distance). Among the seven species examined, *E. fitzingeri* was fastest jumpers (3.41 m s^{-1}), whereas *B. typhonius* was the slowest (1.37 m s^{-1}). Average take-off angle in most species ranged 33–39°, but the angle in *B. orientalis* was small (27°). Take-off speed and jump distance correlated well with both

TM/M_b and HL/SVL, but poorly with IW/SVL (Table 2). The positive correlation between speed and TM/M_b would result from muscle force and power that are generated greater by the more massive muscle in the fast jumpers (Lutz and Rome, '94). Skeletal structure of the hindlimbs determines joint morphology and gear ratio. Because in-lever arms of the hindlimb bones (e.g., the calcaneus) are very small in many anuran species (Choi and Park, '96), the relatively longer hindlimbs indicate more elongated out-lever arms, resulting in higher gear in the fast anurans. The length of the hindlimbs also deter-mines the distance of movement during accelera-tion phase of take-off ('acceleration distance'). The longer limbs therefore are advantageous to

TABLE 2. Regression analyses for morphology-locomotion relationships[1]

Y variable	X variable	a	b (95% CI)	r	P
Take-off speed (m s^{-1})	TM/M_b	0.352	26.699(44.321−9.078)	0.819	0.026
	HL/SVL	−3.280	3.916(5.037−2.794)	0.968	0.0001
	IW/SVL	−1.941	19.533	0.577	0.175
Jump distance (m)	TM/M_b	−0.376	12.537(20.446−4.628)	0.832	0.020
	HL/SVL	−2.081	1.839(2.504−1.173)	0.949	0.001
	IW/SVL	−1.452	9.172	0.472	0.285

Regression equation was presented in the form of Y=a+b∗X and was obtained using the reduced major axis. The 95% confident interval (CI) was given for each slope (b) when a correlation coefficient (r) for that relationship was significant. Significance of r was examined with two-tailed t-test.

increase peak speed at take-off (Gabriel, '84; Choi et al., 2000). There appear few factors affecting gear ratio and acceleration distance other than limb length in the anuran species. However, muscle mass does not simply represent muscle contractile properties. In other words, muscle contractility can vary by the tissue properties like fiber types and fiber arrangements (e.g., pinnation) that differ interspecifically (Putnam and Bennett, '83, Mendiola et al., '91). This would make HL/SVL a better predictor than TM/M_b for speed (r=0.968 versus 0.819, respectively). The narrow inter-ilial width is observed to shape up the anuran body trunk laterally compressed, and is anticipated to allow greater resultant of force vectors exerted by two hindlimbs (Gabriel, '84; Choi and Park, '96). However, despite this morphological assessment, the relative inter-ilial width correlated poorly with speed (r=0.577, P=0.175; Table 2). It may be interpreted that as a part of the pelvic girdle, the ilium is an important attachment site of muscles of the abdominal wall and of the thigh (e.g., iliofibularis, iliofemoralis, triceps femoris) (Duellman and Trueb, '96). The anurans may thus have adjusted the size of the ilia to compromise various mechanical and physiological factors for alert posture or take-off. Because take-off response is largely associated with ecological pressure (e.g., antipredatory behavior) (Hildebrand, '88; Choi et al., '99), morphological components of limbs would also be shaped in accordance with such ecological interactions. Slow anurans have less effective limb morphology for take-off, yet are very successful in the nature by possessing defense mechanisms other than take-off performance (e.g., toxin secretion, coloration) (Daly, '95; Choi et al., '99). Conclusively, anuran take-off speed is portrayed well with high gear (stride rate), acceleration distance (stride distance), and relative contractile potential (force, power, stride rate) characterized by hindlimb length and muscle mass.

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