

Herpetologica, 41(2), 1985, 188-194
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ANURAN LOCOMOTION: FATIGUE AND JUMPING PERFORMANCE

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ABSTRACT: Locomotor performances during 65 consecutive jumps are reported for 10 species of eastern North American frogs. Three species of toads (*Bufo americanus*, *B. fowleri*, *B. terrestris*) did not fatigue, but maintained equivalent performances from beginning to end of the experimental sequences. In contrast, hylids (*Acris crepitans*, *Hyla cinerea*, *H. crucifer*, *H. versicolor*) and ranids (*Rana catesbeiana*, *R. clamitans*, *R. virgatipes*) showed a progressive decline in performance. The onset of fatigue was not directly associated with jumping ability, because some long jumping species showed less fatigue during the experiments than short jumping ones. Captivity has little effect on jumping performance measured at one, five, 10 and 15 days following capture. Most species showed significant differences in jumping performance through time; however, only *B. americanus* had a striking decline in performance.

Key words: Amphibia; Salientia; Bufonidae; Hylidae; Ranidae; Locomotion; Jumping distances; Fatigue; Endurance

JUMPING in frogs supposedly evolved as a behavioral adaptation for rapid escape (Gans and Parsons, 1966; Inger, 1962), yet many terrestrial species hop or jump only short distances and cannot effectively avoid predators by jumping. In contrast,

many semiaquatic and arboreal species can escape from a predator with a single long-distance jump or leap into the water or onto a different branch. Until recently, differences in jumping performance were attributed to an assumed dichotomous dif-

ference in aerobic/anaerobic metabolic capacities. Species that hop (average jumping distance less than five times body length) possessed high aerobic and low anaerobic capacities, whereas species that leap (average jumping distance greater than eight times body length) supposedly possessed low aerobic and high anaerobic capacities (Bennett and Licht, 1974; Hutchison and Miller, 1979; Putnam, 1979; Seymour, 1973). However, this generalization is currently questioned owing to defects in the earlier experimental techniques used for the measurement of locomotor energetics (Hillman et al., 1979) and to a limited taxonomic representation and a failure to consider the diversity of anuran behavior and ecology (Taigen et al., 1982). In fact, a simple dichotomy poorly represents the actual variation in anuran exercise physiology, for all combinations of aerobic and anaerobic capacities occur in frogs (Taigen et al., 1982).

While conducting tests to determine the jumping performances of numerous species of frogs, long jumping species appeared to tire rapidly. These observations and a preliminary analysis (Zug, 1978:Fig. 6) were not conclusive, because not all long jumpers fatigued rapidly, nor was the endurance of some long and short jumping species different. In order to analyze the effect of fatigue on jumping performance more critically, the following experiments examine (1) the effect of sustained activity (consecutive jumping protocol) on jumping performance, (2) the relationship between relative jumping ability and the onset of fatigue, and (3) the effect of time in captivity (periodic jumping protocol) on performance.

MATERIALS AND METHODS

The species tested were: Bufonidae, *Bufo americanus*, *B. fowleri*, *B. terrestris*; Hylidae, *Acris crepitans*, *Hyla cinerea*, *H. crucifer*, *H. versicolor*; Ranidae, *Rana catesbeiana*, *R. clamitans*, *R. virgatipes*. They represent short-, intermediate-, and long-distance jumpers. All frogs were wild caught and were tested within

24 h of capture. The test arena was a 1.5×6 m open-ended, paper-covered track. Temperature in the arena varied from 20–25 C during the two spring testing seasons; however, the daily modal temperature was $22 \text{ C} \pm 1 \text{ C}$. The experimental procedure entailed dipping the frog's hindfeet and pelvic area in nontoxic ink, setting the frog at the entrance of the arena, stimulating the frog to jump, stopping the frog at the final jump in the trial sequence, placing the frog in a container with a shallow layer of water, measuring the distances between consecutive ink marks, and then repeating the procedure until all jumping sequences in a test were made and measured. A more detailed explanation is given elsewhere (Zug, 1978).

A consecutive jumping test consisted of four sequences of 15 jumps each and a final sequence of five jumps. Hence, each test comprised 65 consecutive jumps with a ≤ 2 min pause for measuring between each sequence or trial (1–15, rest, 16–30, rest, 31–45, rest, 46–60, rest, 61–65). The lengths of the first five jumps of each trial (i.e., 1–5, 16–20, 31–35, 46–50 and 61–65) were recorded and are used as a measure of jumping performance at evenly spaced intervals in the jumping sequence. The brief rest intervals (≤ 2 min) are assumed to have minimal effect on the development of or recovery from fatigue (lactate production and muscle glycogen depletion) owing to the 2–9 h required by frogs for their lactate levels to return to normal (resting level) following sustained activity (Hutchison and Miller, 1979). Nonetheless, even this brief rest period may allow some degree of recovery.

The periodic jumping protocol consisted of a trial of 10 sequential jumps recorded on each of four days: the first day, the fifth, the tenth and the fifteenth day following capture. Between trials, each frog was maintained individually in an inflated plastic bag with a piece of moist paper towel. The bags were rinsed and the towels replaced every other day. The frogs were not fed, and the maintenance temperature was the same as the test arena

TABLE 1.—Jumping performance during consecutive jumping trials. Each decimal value is the mean jumping distance (mm) for five consecutive jumps. Sample size is listed beside the scientific name; the integer in parentheses is total number of frogs tested, the preceding integer is number of frogs completing all trials. The relative jumping ability (RJA; jumping distance divided by snout-vent length) is the mean derived from the data of only the first trial. The percent change is the difference between mean performance of the first and the last trial.

Taxon	RJA	Trials					Percent change
		1-5	16-20	31-35	46-50	61-65	
<i>Bufo americanus</i> 22 (22)	4.3	261.1	264.4	246.4	262.0	252.0	-3.5
<i>fowleri</i> 14 (14)	5.1	236.7	229.1	220.7	233.0	226.3	-4.4
<i>terrestris</i> 15 (15)	3.9	171.2	196.8	206.0	196.5	201.3	+17.6
<i>Acris crepitans</i> 30 (35)	21.1	472.6	418.3	386.9	365.6	359.5	-23.9
<i>Hyla cinerea</i> 23 (23)	12.3	456.7	396.3	358.7	359.2	364.1	-20.3
<i>crucifer</i> 24 (24)	19.3	500.1	466.3	459.7	448.1	439.6	-12.1
<i>versicolor</i> 20 (20)	8.3	358.9	354.5	323.2	321.8	283.0	-21.1
<i>Rana catesbeiana</i> 21 (21)	7.8	517.8	481.5	448.9	423.8	402.4	-22.3
<i>clamitans</i> 23 (23)	9.7	644.5	502.8	438.5	398.3	378.3	-41.3
<i>virgatipes</i> 15 (19)	7.8	333.4	285.0	272.9	254.4	235.7	-29.3

(i.e., modal 22 C with 2 C or less fluctuation over five day interval). The laboratory had windows, so the light regime followed the natural progression from March through June.

The mean distance jumped was calculated for each frog at each trial within each test. Variation in jumping performance through time (trials) was tested with an ANOVA-repeated measures design (cross classification with replication; Choi, 1978). Each testing protocol assumes a mixed model; the trials owing to their invariable nature are considered a fixed effect, and the individual frogs as well as their variation in size, sex, motivation, etc. are a random effect. This analysis tests for significance variation in jumping performance among individual frogs and for variation among trials within each species. The ANOVA program used was BMDP2V-analysis of variance for factorial design (Dixon, 1977).

RESULTS

Consecutive Jumping Tests

Bufo americanus and *B. fowleri* showed no evidence of fatigue during the experiments. The means (Table 1) for all five trials were not significantly different; whereas in all other species, the consecu-

tive trial means were significantly different (F_{trials} , $P < 0.01$). Another short-distance jumper (*B. terrestris*) also showed no evidence of fatigue; it jumped further in each of the final four trials than in the first trial, and the performances in these latter trials were nearly constant. Hence, its significant difference among trials derived from the low performance in the initial trial. Strong jumpers, *Acris crepitans* and *Hyla crucifer*, showed declining performance throughout the trials, although the most precipitous reduction occurred between the first and second trial and a smaller, but constant, decline in performance thereafter. A strong jumper, *H. cinerea*, showed also a large difference between the first and second trials, although the performance in the final three trials was nearly equivalent. The moderate jumpers (*Hyla versicolor*, *Rana catesbeiana*, *R. clamitans* and *R. virgatipes*) showed a monotonic reduction in performance. The decline in jumping distance was most precipitous for *R. clamitans* and least in *H. versicolor*. These four species also had the greatest decline between the first and second trials.

An evaluation of intraspecific jumping performance revealed considerable variation between individual frogs of the same species. In all species tested, the F values

TABLE 2.—Jumping performance during time-in-captivity trials. Each value is the mean jumping distance (mm) for 10 consecutive jumps.

Taxon	n	Day of test				Mean intertrial difference
		1st	5th	10th	15th	
<i>Bufo americanus</i>	22	262.8	217.6	195.9	191.1	23.9
<i>fowleri</i>	14	232.9	237.5	237.2	211.3	10.4
<i>terrestris</i>	15	184.0	204.8	199.1	194.5	10.4
<i>Acris crepitans</i>	33	437.6	513.4	450.5	437.2	50.7
<i>Hyla cinerea</i>	23	426.9	502.5	480.6	388.2	63.3
<i>crucifer</i>	23	492.8	516.4	527.6	478.8	27.9
<i>versicolor</i>	20	356.7	300.2	305.7	308.4	21.6
<i>Rana clamitans</i>	16	527.2	501.9	590.1	599.4	40.9
<i>virgatipes</i>	14	279.0	316.0	301.6	282.0	23.7

were highly significant ($P < 0.01$) and emphasized the high variability of jumping performance within a species.

In all the tests, there was a significant interaction ($F_{\text{interaction}}, P < 0.01$) between the individual frog's jumping performance and the results of each consecutive trial. Specifically this portion of the ANOVA examined the variability of an individual frog's performance in successive trials. Thus, all species showed variable performance from trial to trial, although in the short-distance jumping *Bufo americanus* and *B. fowleri*, the variation of performance did not alter the average performance in successive trials.

Effects of Captivity

The amount of time spent in captivity had less effect on jumping performance (Table 2) than did consecutive jumping (Table 1). Only *Bufo americanus* showed a monotonic decline in jumping performance. The performance of *Hyla versicolor* declined from the first to the second trial, but thereafter performance remained roughly constant; in contrast, *B. terrestris* showed an initial improvement then a constancy of performance. *Bufo fowleri* maintained a fairly uniform performance across the four trials. *Acris crepitans*, *Rana virgatipes* and *Hyla cinerea* improved their performance in the second trial, and performance declined thereafter; *R. clamitans* showed just the opposite pattern with an initial decline and im-

provement thereafter. *Hyla crucifer* improved its performance through the first three trials, then declined. These patterns of performance are diverse and seem not to be linked by a single trend.

The intraspecific variability of jumping performance mirrored that observed for the consecutive jumping trials. The performance of each individual frog was highly variable, and the same factors affecting the variability within a sequence of leaps apparently affected performance through time.

In contrast to the high intraspecific variation, the variation between trials was lower. Seven species possessed statistically significant intertrial variation ($F_{\text{trials}}, P < 0.05$ for *Bufo fowleri*, *Hyla crucifer*, *H. versicolor*, *Rana clamitans* and $P < 0.01$ for *B. americanus*, *Acris crepitans*, *H. cinerea*). The patterns of intertrial variation are described above, and no single explanation seems adequate. Certainly, the intertrial variation as measured by average intertrial difference (Table 2) was little different for the two species (*B. terrestris*, *R. virgatipes*) lacking statistical significant variation than for the species with comparable jumping performances and showing statistical significance.

All species in the time-in-captivity tests possessed statistically significant interaction ($P < 0.01$) in individuals' jumping performances in successive trials. The variability of performance seemed to be largely "random" or at least uniformly

distributed around a mean jumping distance for each frog species.

DISCUSSION

The frogs tested herein segregate into two classes: (1) a group showing no or slight degradation (i.e., performance of any successive trial differs <5% from that of the first trial) of jumping performance; (2) a group showing a moderate (10–19% difference) to strong ($\geq 20\%$) degradation of performance. The first group contains only the toads (*Bufo*), and they are typically characterized physiologically by high aerobic-low anaerobic metabolism during continuous, short-distance locomotion (Bennett and Licht, 1974; Taigen et al., 1982). The data of toad performance are consistent with the low fatigue characterization, because the ranges of jumping distances are concordant for the first and last jumping trials (e.g., 76–386 mm and 96–365 mm, respectively, for *Bufo americanus*). The second group, which showed declining performance, is not homogeneous, and the continuum in degree of endurance supports the interpretation that the aerobic-anaerobic contribution to locomotor energetics varies continuously, not dichotomously, among anuran species (Taigen et al., 1982). Furthermore, the performance data show the absence of an inverse correlation between performance and endurance. For example, *Rana clamitans* is a moderate jumper, yet it has the greatest degradation of performance from first to fifth trial; in contrast, *Hyla crucifer* is a strong jumper and has the least degradation of performance. The latter species is a particularly good example of the unrealistic nature of the assumed association in long jumping species of rapid fatigue with high anaerobic scope. The high performance, relatively high endurance, and high aerobic dependence index (ADI; Taigen et al., 1982:Table 4) of *H. crucifer* well demonstrates the fallacy of that assumption. Clearly, relative jumping ability or average jumping performance is an unreliable predictor of a species' endurance.

Based on the rate of performance degradation and the percent difference in performance between the first and fifth trial (Table 1), the endurance ranking is: *Bufo* species; *Hyla crucifer*; *H. cinerea*, *H. versicolor* and *Rana catesbeiana*; *Acris crepitans*; *R. virgatipes*; *R. clamitans*. This ranking shows a pattern similar to the physiological ranking of Taigen et al. (1982:Table 4) based on the aerobic dependence index (ADI) and allows the postulation that the *cinerea-catesbeiana* group will likely possess a low, positive ADI, and *A. crepitans* a low, negative ADI. *R. virgatipes* and *R. clamitans* are predicted to possess a moderate, negative ADI.

Bufo americanus and *B. fowleri* were the only consistent performers throughout the sequence of 65 consecutive jumps. The other anurans showed intertrial variability. A comparison of the average difference between successive trials shows a general consistency of performance for *B. americanus*, *B. fowleri* and *B. terrestris* (excluding its first trial results). Their average differences between trials were approximately 10 mm; whereas, these differences were greater than 15 mm in all other anurans tested. *Rana clamitans* and *Acris* showed monotonic declines and had average intertrial differences of 66.6 and 28.2 mm, respectively. The other species had averages ranging from 15–29 mm, and most showed the greatest decline in performance between the first and second trial with a leveling off thereafter.

An examination of the variability of locomotor performance shows little difference in the ranges of jumping distances in the first and last trials, except in the low endurance species, and even in these latter species, only the upper limit shows a striking drop. The lowering of the upper limits reduces intratrial variability (as measured by standard deviations) in the long-distance jumping/low endurance species. Thus, fatigue does not cause erratic performance but does cause a lessening of exertion per unit time.

As a measure of endurance, jumping

performance possesses a greater variability than does whole body lactate content. *Bufo americanus* has a coefficient of variation for lactate content (calculated from Taigen et al., 1982) of 1.7 and a coefficient for mean jumping distance (in fifth trial) of 25.0. In *Hyla crucifer*, these coefficients are 1.1 and 24.6, respectively; a comparison of jumping distance variation in similarly sized *Rana* (*sylvatica* and *virgatipes*) gives 22.2 and 32.6, respectively. Part of this difference in variability likely results from the constancy in timing and intensity of the experimental procedure in the physiological tests in contrast to the fluctuation of these aspects in the behavioral tests. A constant-speed rotating chamber requires a regular and equal-efforted jump or righting response; the proximity and approach of a human hand may well elicit different escape behaviors at different times.

The time-in-captivity experiments do not measure fatigue. Obviously a frog sitting undisturbed in captivity will not develop an oxygen debt or accumulate lactic acid. The experiments test for training (i.e., potential improvement of performance through time) and for lethargy (i.e., potential accustomization and failure to respond maximally to stimuli). The performance for seven species showed a statistically significant modification in jumping distances throughout the 2 wk of captivity (Table 2). This significance reflects intertrial variability rather than a monotonic change (either increase or decrease) in jumping performance. Both *Acris crepitans* and *Rana virgatipes* jumped the same average distance in the first and the last trial and only the former showed a statistically significant difference between trials. *Bufo americanus* and *R. clamitans* had a change of 72 mm between first and last trials (decrease and increase, respectively). Overall, two species showed no or slight change in jumping performance from beginning to end, five species decreasing performance, and three species increasing performance. Hence, no pattern is evident for the majority of

species (only *B. americanus* possessed a monotonic trend) and the results seem to reflect a randomness of the data sets. What is the cause of this randomness or high variability? Because the trials extend over a 15 day period, differences in ambient temperature might account for some of the variability. Testing procedure may have differed from trial to trial, although the same individual performed all the tests. Even though the intertrial results are variable, they do not show a decline in performance and are concordant with the absence of an altered metabolism during captivity (Taigen et al., 1982).

The importance of time-in-captivity data is the general absence of an effect on performance by length of captivity. Hence, the numerous behavioral and physiological tests are likely compatible and comparable whether the animals tested were fresh caught or laboratory held.

Acknowledgments.—Numerous individuals have contributed to the perpetuity of my frog locomotion studies, and I am continually thankful for their assistance and encouragement. Joan Dudley tested the frogs again and again; Lee-Ann Hayek advised me in statistical protocol; Albert F. Bennett, Charles Crumly and W. Ronald Heyer offered advice and editorial criticism; Theodore L. Taigen greatly assisted me in the physiological interpretation of the behavioral data and, with several anonymous reviewers, tempered my excessive speculations. I sincerely appreciate the assistance and advice of all.

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Accepted: 30 September 1984
Associate Editor: James Spotila

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