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Lightening the Load: Micturition Enhances Jumping Performance of Squirrel Treefrogs

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Lightening the Load: Micturition Enhances Jumping Performance of Squirrel Treefrogs

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Arboreal amphibians are prone to desiccation and exhibit a variety of adaptations that reduce the influence of hydric stress in the arboreal habitat (see Shoemaker et al., 1992 for review). In addition to possessing adaptations that reduce water loss, many species store urine as a source of water during dry periods (Ruibal, 1962; Shoemaker et al., 1992).

Water, stored as dilute urine in the bladder, appears to play an important role in allowing terrestrial and arboreal frogs to survive dry environmental conditions (Ruibal, 1962; Shoemaker, 1964; Claussen, 1974a). Individuals of the squirrel treefrog (*Hyla squirella*) experience seasonal drought in their natural environment (September–November: Buchanan, 1988). During these periods, frogs must rehydrate regularly from water sources such as dew and soil moisture. Frogs that do not obtain or store sufficient quantities of water may not survive highly desiccating diurnal conditions (e.g., Ruibal, 1962; Shoemaker, 1964) or may have their nocturnal activity restricted (e.g., Pough et al., 1983).

The importance of water stored in the bladder suggests that treefrogs would be unlikely to void their bladders except when there is a ready source of water available for rehydration. However, even during dry periods, many frogs (especially bufonids and hylids) void their bladders when approached or seized by potential predators (Duellman and Trueb, 1986; pers.

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obs.). One potential benefit of such seemingly maladaptive behavior is enhanced ability to escape predation. There are two non-mutually exclusive ways that voiding the bladder could enhance escape from predators: (1) voiding urine reduces the mass of the frog allowing it to jump farther away from the predator (Claussen, 1974b), and (2) urine contains chemicals that either repel, attract or confuse predators, allowing the frog to escape (Duellman and Trueb, 1986; Endler, 1986). In this study we tested the first mechanism using squirrel treefrogs because they can store large quantities of water in their bladders relative to their empty bladder mass (>30% of empty bladder mass: pers. obs.) and they frequently void the contents of their bladders when approached by humans (pers. obs.). We tested the hypothesis that these frogs can significantly increase the distances they can jump by reducing their mass through voiding urine stored in their bladders.

The prediction that a reduction in the mass of water stored in the bladder will increase distance jumped is based on the simple ballistic equations frequently used to model saltation in frogs (see review in Marsh, 1994). These models predict that if all variables that affect jump distance except mass or the center of mass in the body are held constant, a decrease in mass will increase the distance jumped by the frog. Thus, it is necessary to demonstrate that (1) micturition is a common response by frogs to perceived threat, (2) there is biologically relevant variation in mass associated with micturition, and (3) that variation in mass is not compensated for during a jump by variation in other variables, resulting in no systematic variation in distance jumped.

We collected adult, male squirrel treefrogs in St. Landry Parish, Louisiana during June 1992 and maintained them in the laboratory until this experiment was performed (31 January–8 March, 1993). The frogs ($N = 24$) were housed in individual 11 screen-topped containers on a natural photoperiod at 24 ± 1 C and were fed 2–3 week old crickets, *Acheta domesticus*, ad libitum (Buchanan and Jaeger, 1995).

We initially performed a pilot study to determine whether or not micturition is a common response to a potential threat, as we had observed in the field. In this study 10 frogs were placed in the jump arena described below and approached from behind by the observer's hand (Rand, 1952; Zug, 1978). Six of the 10 frogs voided their bladders prior to jumping. This effect diminished rapidly over time as frogs appeared to become accustomed to human activity and manipulation while maintained in the laboratory. We tested the influence of jump order (Zug, 1978) on distance jumped by frogs with empty bladders prior to our primary experiment by forcing each of 21 frogs to make five non-consecutive jumps over the course of 4 h on the same day. We analyzed the data using Friedman's test and Tukey-type multiple comparisons (Zar, 1984; $N = 24$, $\alpha = 0.05$).

We controlled for individual variability in jumping ability that might be due to size (Rand, 1952; Rand and Rand, 1966; Zug, 1978) or other variables by comparing the jumping ability of an individual when its bladder was full to the jumping ability of the same frog when its bladder was empty. Because we could not force frogs to retain the contents of their bladders during jumps, we allowed the frogs to jump sponta-

neously 12 times (on different occasions), and we then compared the average distances of jumps that met our criteria for either "empty" or "full" bladder jumps. Frogs were described as having empty bladders when the mass of the water they retained in the bladder during a jump was <10% of their "standard mass" (mass with empty bladder; Ruibal, 1962) and as having full bladders when the mass of the water carried during a jump was >18% of their standard mass (mean ± 0.5 SD). All jumps with urine mass within 0.5 SD of the mean were excluded from the analysis. Three frogs were removed from the experiment due to illness, and frogs not having at least one jump in both categories (empty or full) were excluded from the analysis, leaving a sample size of 17 frogs.

We conducted jumping trials from 0700–1000 h because most frogs typically rehydrated before 0700 h daily. Tests were performed at 24 ± 1 C, a temperature below the optimum for muscle activity in this species (John-Alder et al., 1988; Marsh, 1994) but within the normal activity range for this species (Buchanan, 1988; John-Alder et al., 1988). We determined the mass of each frog by allowing it to crawl directly from its chamber onto an electronic balance. We obtained the masses of frogs before and after a jump and recorded whether or not a frog voided its bladder at any time. The person recording the jumps of the frogs did not know the identity, masses, or bladder states of the frogs selected in random order and the person determining the masses of the frogs did not know the jump performance or bladder states of the frogs after they had jumped.

The jump arena (1.5 \times 0.5 \times 0.2 m) was covered in black, plastic sheeting and was positioned in a light-safe area. The release point of the frog was 1.3 m from a white acrylic panel illuminated from behind by an incandescent light. The frogs moved unidirectionally toward the illuminated panel (at release point 0.5 lx from side walls and 125 lx from panel) as they are photopositive at these illuminations (Jaeger and Hailman, 1973). We placed the open box containing the frog on its side at the release point allowing the frog to jump spontaneously toward the light. It was occasionally necessary to encourage a frog to jump by gently touching the cloacal region of the frog with a soft brush bristle embedded in a thin, plastic rod (Jaeger and Hailman, 1973). Once a frog jumped, we measured the distance between the original and final position of its cloaca. Rarely, a frog jumped <150 mm (4.8% of all jumps were <150 mm in the study of jump order effects) and was forced to jump again until it jumped at least 150 mm. Forcing frogs to repeat very short jumps could only bias the outcome of this experiment toward not finding differences between full and empty bladder jump distances.

After a frog jumped, its mass was obtained, its bladder was purged twice, and the mass of the frog was obtained again. Previously, we compared the amount of fluid forced from the bladders of frogs in each of four consecutive purges. A median of 86% (interquartile range: 70.9–95.5%, $N = 26$) of the total fluid that could be removed from the bladder in four purges (using a canula for the fourth purge) was voided in the first purge and a median of 100% (interquartile range: 97.6–100%) was voided by the second purge. We compared the average distance jumped by a frog when it had a full bladder to the average distance

jumped by the same frog when it had an empty bladder using the paired t test (one-tailed, $N = 17$, $\alpha = 0.05$) as the data met the assumptions of this test (Zar, 1984). We employed a one-tailed test of the hypothesis because we predicted a priori that frogs would jump farther with empty bladders than with full bladders.

In the test of jump order, frogs jumped significantly farther in the first jump than they did in the last two of five jumps ($\chi^2 = 17.9$, $P = 0.0013$, $N = 24$, Table 1). Therefore we tested frogs not more than once per day or twice per week. We found no statistically significant relationships between measures of body size (SVL and tibiafibula length) and maximum distances jumped by individuals which were used in the second experiment (SVL: $r_s = -0.334$, $P = 0.139$, $N = 21$; tibiafibula length: $r_s = -0.173$, $P = 0.452$, $N = 21$). The statistical power of both of these tests to detect small (0.20), medium (0.50), and large (0.80) effect sizes was 22%, 77% and 99.5% respectively (Cohen, 1988). Thus it is likely that variation within and among individuals in jump distance obscured any effects of body size.

Some squirrel treefrogs voided their bladders entirely in response to a perceived threat whereas others retained part or all of their bladder volume during jumps. The amounts of urine carried in frogs' bladders during jumps ranged from 0–59.7% of standard mass with an average of 13.9 \pm 7.72% (original standard masses—range: 1.09–2.38 g, mean: 1.72 \pm 0.34 g). The greatest quantity of urine carried by an individual relative to its mass (59.7%) was 0.71 g by a frog with a standard mass of 1.19 g. The distances jumped (considering all jumps, $N = 274$) by frogs ranged from 150–620 mm with an average of 343 \pm 97 mm. The average SVL of frogs was 30.9 \pm 1.94 mm; thus, an average jump was equivalent to about 11 body lengths. The greatest distance jumped by a frog (620 mm) was equivalent to a jump of over 20 body lengths (30.1 mm SVL).

Frogs were able to jump significantly farther when their bladders were empty (363.2 \pm 70.9 mm) compared to when full (306.6 \pm 82.6 mm, Fig. 1, $t = 2.61$, $P < 0.01$, $N = 17$). Based on the difference in the overall mean distances jumped, frogs with empty bladders jumped 18.5% farther than frogs with full bladders. However, when considered for each frog

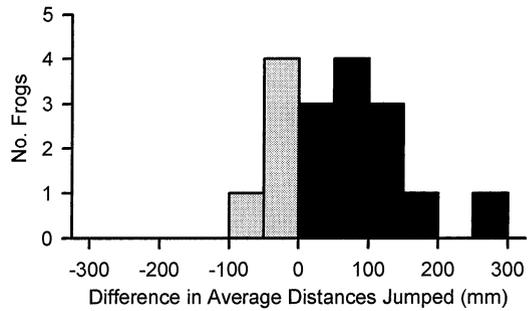


FIG. 1. The distribution of differences in the average distances jumped by frogs when they had empty versus full bladders (=empty bladder jump distance–full bladder jump distance). Grey bars represent the frequencies of frogs that jumped farther with full bladders; black bars represent the frequencies of frogs that jumped farther with empty bladders.

individually (Fig. 1a), frogs jumped, on average, 26.4 \pm 42.71% farther with empty bladders than with full bladders (range: –28.6 – 143%, negative values represent those cases when frogs jumped farther with full bladders than with empty bladders, Fig 1).

The distance that a squirrel treefrog can jump is seriously reduced by the presence of large quantities of water stored in the bladder. In our experiment, frogs were able to jump significantly farther when they voided their bladders than when they jumped with full bladders. The difference in the average distance jumped translates into at least a two body-length (about 20–25% of an average full bladder jump) increase in distance jumped, on average, for frogs that void their bladders. Such an increase in distance jumped may be substantial when a frog is evading predators such as snakes (snakes and invertebrates are probably the most important predators on *H. squirella*, pers. obs.).

We consider this estimate to be conservative, however, as the frogs used in this study had been maintained in the laboratory and were seemingly accustomed to human presence and disturbance. We found no statistically significant relationships between measures of body size and the maximum distances jumped by frogs in a preliminary analysis as would be expected if the frogs were jumping at their maximum capabilities (Rand and Rand, 1966), although our frogs did not represent a very great range of body sizes. Also, the value of the average distance jumped by frogs in our study was only 60% that reported for the same species by Zug (1978) suggesting that our frogs were jumping submaximally. Frogs unaccustomed to human presence may jump farther under all conditions due to a stronger avoidance response; under more natural conditions, such an increased response may magnify the effects that we observed (Rand, 1952).

Our results also have implications for evaluating the results of other studies of jumping in frogs. Our data demonstrate clearly that it is necessary to control for, and report, bladder volume and micturition when studying the effects of other constraints on jumping performance. Substantial uncontrolled variation as-

TABLE 1. Tukey-type multiple comparisons of the distances jumped in each of five repeated, non-consecutive jumps by individual squirrel treefrogs. Median distances jumped are provided in Fig. 1.

Jump no.	Jump no.	q	P
1	versus 2	1.49	>0.1
1	versus 3	3.55	<0.1
1	versus 4	5.10	<0.005
1	versus 5	4.39	<0.025
2	versus 3	2.07	>0.1
2	versus 4	3.62	<0.1
2	versus 5	2.91	>0.1
3	versus 4	1.55	>0.1
3	versus 5	0.84	>0.1
4	versus 5	0.71	>0.1

sociated with bladder volume could swamp out biologically meaningful effects of other factors that might affect jump performance. It is probable, however, that testing frogs immediately after collection may reduce this variance because of the tendency for the frogs to void their bladders prior to testing.

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**Resolution of the
Taxonomic Status of
Nectocaecilia haydee (Roze) and a
Revised Key to the Genera of the
Typhlonectidae
(Amphibia: Gymnophiona)**

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Study of the aquatic and semiaquatic caecilians of the Neotropical Typhlonectidae has been hampered by a lack of clearly differentiated species and genera. These taxonomic problems are most clearly demonstrated by the description of numerous species that subsequently have been synonymized with older names, sometimes in different genera (Nussbaum and Wilkinson, 1988; Wilkinson, 1988, 1989, 1991). Herein I consider the status of *Nectocaecilia haydee* (Roze) which constitutes the outstanding problem in the taxonomy of the typhlonectid genus *Nectocaecilia* (Nussbaum and Wilkinson, 1989). I also present a revised key to the genera of the Typhlonectidae.

Taylor (1968) established the family Typhlonectidae for the species of *Typhlonectes* and *Chthonerpeton*, whose affinities had long been recognised (Peters, 1879). Taylor further established the new typhlonectid genus *Nectocaecilia* to include *C. petersii* Boulenger, designated as the type species, *C. haydee* Roze, and two new species *N. ladigesi* and *N. fasciata*. All of these were known only from their holotypes. Taylor (1970) described *N. cooperi*, also based on a single specimen, and Taylor (1971) reported on two additional specimens of *N. ladigesi*.

The concept and content of *Nectocaecilia* has been problematic since its inception. Taylor (1968) intended the genus to accommodate those typhlonectids that have anteriorly placed tentacles (as in *Typhlonectes*)