SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739–747.

TENNESON, M. G. 1983. Behavioral Ecology and Population Decline of the Mink Frog, *Rana septentrionalis*. Unpubl. master's thesis, University of North Dakota, Grand Forks.

VIETES, D. R., S. NIETO-ROMÁN, M. BARLUENGA, A. PALANCA, M. VENCES, AND A. MEYER. 2004. Post-mating clutch piracy in an amphibian. Nature 431:305–308.

WELLS, K. D. 1977a. The social behavior of anuran amphibians. Animal Behaviour 25:666–693.

———. 1977b. Territoriality and male mating success in the Green Frog (*Rana clamitans*). Ecology 58:750–762.

———. 1978. Territoriality in the Green Frog (*Rana clamitans*): vocalizations and agonistic behavior. Animal Behaviour 26:1051–1063.

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Calling Behavior and the Capacity for Sustained Locomotory Exercise in the Gray Treefrog (*Hyla versicolor*)

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ABSTRACT.—**Vocal advertisement by male anurans can make considerable demands on an individual's energetic reserves and innate physiological resources. In this study, we tested for a relationship between calling and locomotory performance in male Gray Treefrogs, *Hyla versicolor*. Male vocal activity was monitored in choruses assembled in an artificial pond and call duration and pulse effort used as calling performance metrics. Swimming distance served as our measure of locomotory performance. When males were compared within experimental choruses, there was no tendency for the male that produced the longest calls to swim further than the male that produced the shortest calls. Rather, the opposite was true. When these same males were ranked based on their pulse effort, we found that the male with superior calling performance also performed better in the swimming test than the male that gave fewer total pulses. There was no significant relationship between male condition (weight relative to length) and either calling or swimming performance. We hypothesize that pulse effort, which shows more stability within males under dynamic acoustic situations in choruses than call duration, may better reflect limitations of the cardiovascular and respiratory system than does call duration.**

In many species of anuran amphibians, vocal advertisement for mates represents the most energetically demanding activity of males during the adult phase of the life cycle (Ryan, 1988; Pough et al., 1992; Prestwich, 1994; Grafe and Thien, 2001; Wells, 2001). For example, in temperate zone hylids such as the Spring Peeper, *Pseudacris crucifer*, and the Gray Treefrog, *Hyla versicolor*, or Neotropical *Hyla microcephala*, the energetic cost of average rates of calling can often exceed 10 times resting metabolic rates (see table 14.8 in Pough et al., 1992). Studies of the physiological and morphological basis of acoustic signaling in such species have documented a suite of adaptations that support its potentially enormous energetic demands (Taigen et al., 1985; Marsh and Taigen, 1987; Bevier, 1995; Ressel, 1996, 2001; Zimmitti, 1999; Girgenrath and Marsh, 2003), whereas behavioral studies have addressed ultimate explanations (reviewed in Gerhardt, 1994; Sullivan et al., 1995; Schwartz, 2001) as well as strategies that allow males to modulate the cost of advertisement in ways that do not compromise a male's ability to attract a female (Wells, 1988; Schwartz et al., 1995).

In this study, we tested for a relationship between performance measures of two kinds of energetically demanding physical activity in the same individuals of *H. versicolor*: (1) calling performance, as indicated by (a) the number of pulses in the call (i.e., call duration) or (b) pulse effort (pulses per call × calling rate); and (2) locomotory capability, as indicated by swimming

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distance. Our rational was that, because calling behavior is intimately related to male fitness (e.g., Klump and Gerhardt, 1987) and perhaps genetic quality (Welch et al., 1998; Welch, 2003), components of calling might also reflect an overall capacity for prolonged physical activity. Both calling and swimming are relevant to the behavioral ecology of Gray Treefrogs. Males call from shrubs or trees bordering wetlands or may be found vocalizing on mats of vegetation on the surface of ponds and postamplectant males must swim following egg deposition by females. Call duration in the Gray Treefrog is a call feature that shows repeatable differences among individual males (Runkle et al., 1994; Schwartz et al., 2002) and influences female choice both in the laboratory (Sullivan and Hinshaw, 1992; Gerhardt et al., 1996) and in the wild (Schwartz et al., 2001). Moreover, artificial crosses suggest that males that give long calls may sire offspring that have fitness enhancing developmental characteristics as compared to males that give shorter calls (Welch et al., 1998; Welch, 2003). Tadpoles from such crosses also spend more time in feeding activity (Doty and Welch, 2001). Pulse effort tends to be a less variable attribute of calling within males (e.g., Schwartz et al., 2002) and is a measure that reflects energetic expenditure over a longer block of time than does call duration. Swimming relies primarily on the activities of the leg muscles and, although adult males may spend only a small proportion of their time in the water, it is likely that the ability to sustain movement in water is positively correlated with endurance while moving through the vegetation matrix in a forest or along a shoreline (e.g., during foraging or traveling from feeding sites to a pond).

MATERIALS AND METHODS

We captured our test subjects at a pond at the Baskett Wildlife Area near Ashland, Missouri, between 2030 and 2400 h from mid-May until early July. The following morning, we marked (numerically with a freeze-brand on the back and a toe clip pattern), weighed (to nearest 0.01 g), and measured (SVL and tibiafibula to nearest 0.001 inch using a Vernier calipers) the animals. Prior to weighing each male, we emptied its bladder by applying pressure gently to its midsection and then blotted it dry. Subsequently, the males (up to 30) were released in a screened-in octagonal artificial pond located in a greenhouse at the University of Missouri (2 m on each side; see fig. 3 in Schwartz et al., 2001). Opaque plastic sheeting blocked extraneous light from the pond and acoustic foam wedges (Soundcoat, Inc.) surrounding the outer base of the enclosure reduced sound echoes.

That evening we broadcast (approximately 75 dB SPL, Fast RMS, C-weighting at center of pond) a tape recording of a natural chorus of *H. versicolor* from two speakers (Realistic 40-1242) suspended outside the enclosure. Our goal was to acoustically stimulate at least eight males to call; however, this was not always possible. After calling in the chorus appeared sustained and fairly vigorous, we positioned individual males under a screen cage on top of each of up to eight cinderblocks that were equally spaced around the periphery of the pond. We then removed the additional treefrogs from the pond, waited for our subjects to resume stable calling, and then turned off the sound stimulus.

We used a computer-based call-monitoring system to acquire data on the vocal behavior of the males (for technical details, see Schwartz, 1993, 2001). Calls were detected with directional microphones that faced each cage and were linked to a custom battery-powered interface board that sent its output to a computer (Commodore Amiga 600) via its parallel port. The sampling rate of the computer (100 Hz) and the temporal resolution settings of the hardware interface were adjusted so that we could resolve individual pulses within the calls of each of our subjects. We acquired three consecutive 10-min data files from each of 10 choruses and one 10-min file from a single chorus caused by a technical problem. Males were then used for additional playback experiments outside the scope of this study. The next morning, data files were analyzed using custom software and programs written in SAS to calculate the average call duration (e.g., pulses per call) of each male. Based on this analysis, one of us (JJS) identified the male that had given, on average, the longest and the male that had given the shortest calls in the greenhouse chorus. These two males were transported in plastic containers to an indoor laboratory for a test of swimming distance, usually the day following calling.

All swimming tests were made by the author "blind" to the calling behavior of the two subjects (KMR). Each male, after a 20–30-min period in which to equilibrate to the water temperature, was forced to swim until exhaustion in an open-ended Plexiglas chamber positioned within a larger fiberglass trough (Fig. 1). The trough was partially filled with water (depth ~ 3.0 cm) adjusted to 20°C using warmer water and crushed ice. Temperature was checked and readjusted, if necessary, between swimming tests. Because the water temperature was adjusted to within about 1–2°C of room temperature, the bath temperature remained quite stable (within 1°C) for the duration of swimming bouts. To encourage subjects to swim, they were prodded on their rear with the tip of a metal probe. Because the power required

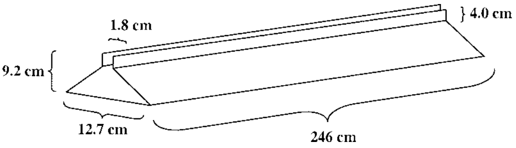

FIG. 1. Diagram of the Plexiglas swimming chamber. The chamber was open at the top so that the frogs could be prodded with a metal probe. The openings at each end allowed water to enter the apparatus. During tests, the swimming chamber was partially submerged within a fiberglass trough (365.8 × 39.4 × 106.9 cm).

to move through water increases nonlinearly with velocity (Rome et al., 1992), forcing males to swim as fast as possible could seriously compromise swimming distance. Moreover, endurance during exercise declines with velocity (Gatten et al., 1992). Accordingly, in these trials, males were allowed to choose their own swimming velocity and prodding occurred only if a subject failed to move his hind legs. Whenever a male reached the end of the central chamber, he was expeditiously turned around and encouraged to swim back in the other direction. We defined exhaustion as the point at which a frog would not respond to prodding for 15 sec.

We completed swimming tests with 11 pairs of males monitored in the artificial pond. We performed paired analyses (Wilcoxon Matched-Pairs Signed-Rank Test) to test the null hypothesis that the males that had given calls with the greatest average number of pulses swam further than the male who had given fewer pulses per call. A paired analysis was used because the acoustic environment, which differed among nights, can have a profound effect on the call duration and, to a lesser extent, pulse effort of males (Wells and Taigen, 1986; Schwartz et al., 2002). Swimming distance was calculated as both the number of laps and number of laps relative to body size. We used tibiafibula length as our measure of size because measurements of this feature have a higher repeatability than those of SVL (Murphy, 1994; B. W. Buchanan, unpubl. data). This choice did not produce qualitative changes in our findings. In addition to testing for a relationship between call duration and endurance, we evaluated the significance of total pulses (i.e., pulse effort) given during the 30-min monitoring period. For this analysis, we reranked the two exercised males according to this calling attribute. We examined the importance of a male's condition on his calling and swimming performance by using for our measure of condition the residual from the linear regression of weight against tibiofibula length. For the regression analysis, we used data on all 275 males monitored in the artificial pond.

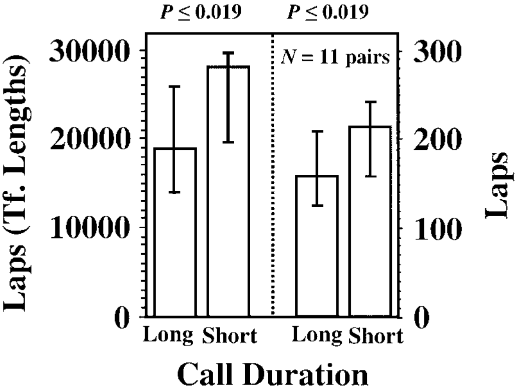

FIG. 2. Swimming distance (medians and interquartile ranges) of the male that produced on average the longest (mean of averages = 21.0 pulses, median of averages = 20.4, range of averages = 16.3–26.5) and the shortest calls (mean = 14.2, median = 13.3, range = 10.1–23.5) in the artificial pond (N = 11 pairs). Right bins: distance in laps (lap = 246 cm). Left bins: distance in tibiafibula lengths of the swimmer. P-levels are for a two-sided Wilcoxon Matched Pairs Signed Rank Test.

RESULTS

Males swam an average of 181 laps (median = 187, range = 82.5–285.0, N = 22) and produced calls with an average of 17.6 pulses (mean of averages, median of averages = 16.9, range of averages = 10.1–26.5). Mean pulse effort was 11859 per hr (median = 11,342, range = 6348–19,134). The time of the swimming trials ranged from 102–170 min (mean = 131.7, median = 129) and male swimming velocities (mean = 1.66 laps/min, median = 1.60) fell within a fairly narrow range (1.38–2.01 laps/min). There was no tendency for the male that produced longer calls to swim further than the male that produced shorter calls. In fact, the opposite was true (Fig. 2; means: 19,064.8 vs. 24,524.5 tibiafibula lengths, medians: 18,648.2 vs. 27773.3, $P \leq 0.019$, two-tailed Wilcoxon Matched-Pairs Signed-Rank Test on tibiafibula lengths swam). When males were ranked according to pulse effort, we found that males that had produced more pulses also swam further than males that produced fewer pulses (Fig. 3; means: 23,916.0 vs. 19,673.3 tibiafibula lengths, medians: 25,640.4 vs. 18,648.2, $P \leq 0.042$), although there was no relationship between the difference in pulse effort and the difference in swimming distance among paired males ($R_S = 0.055$, $P = 0.873$). The two measures of calling behavior we quantified (call duration and pulse effort) were not significantly negatively correlated when we pooled data from all nights (N = 22 males). Moreover, males were no more likely to differ in their ranking for call duration and pulse effort than they were to be

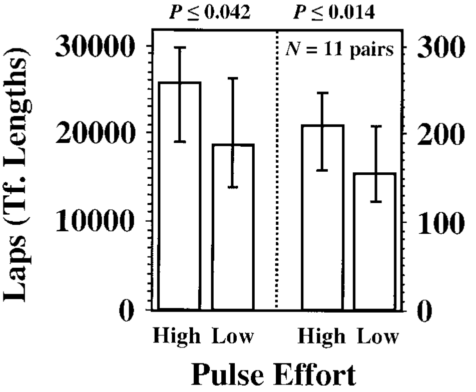

FIG. 3. Swimming distance (medians and interquartile ranges) of males when members of each pair were ranked based on pulse effort rather than call duration (N = 11 pairs). Right bins: distance in laps (lap = 246 cm). Left bins: distance in tibiafibula lengths of the swimmer. P-levels are for a two-sided Wilcoxon Matched Pairs Signed Rank Test. Males ranked first (High) produced an average of 7165.4 pulses (median = 7031.0, range = 5574–9567). Males ranked second (Low) produced an average of 4693.4 pulses (median = 4784.0, range = 3174–6237).

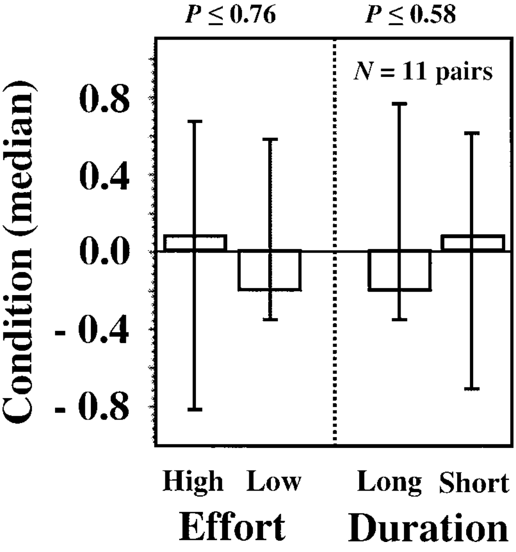

FIG. 4. Condition (medians and interquartile ranges; see text) of males ranked within pairs as high or low in pulse effort (left) and longest or shortest in average call duration (right). P-levels are for a two-sided Wilcoxon Matched Pairs Signed Rank Test.

ranked similarly: on four nights the male that ranked lowest for call duration within his chorus was also the lowest ranking male for pulse effort, whereas on seven nights the lowest ranking male for call duration produced the most pulses (one-tailed binomial test, P = 0.2744).

The median condition of males that ranked first in call duration was slightly lower than that of males that ranked second, and the median condition of males that ranked first in pulse effort was slightly higher than that of males that ranked second (Fig. 4). However, neither of these differences was statistically significant. The male in best condition did not swim significantly further than the male ranked second in condition (Fig. 5).

DISCUSSION

In *H. versicolor,* males that produce long calls are preferred by females to those producing short calls and also may be carrying genes that positively impact larval fitness under certain environmental conditions (Welch et al., 1998; Doty and Welch, 2001). However, in our experiment, such males did not exhibit a greater capacity for prolonged exercise, as reflected by swimming distance, than males that ranked low in call duration. Rather, males using the longer calls swam less. When males were ranked using pulse effort, results were the opposite. What could explain these findings?

In male treefrogs, calling and swimming rely on different sets of muscles (Marsh, 1999). In general, the muscles associated with calling (trunk and laryngeal muscles) are characterized by predominantly oxidative (fast twitch) fibers, with relatively high mitochondrial densities and enzyme activity levels comparable to those of aerobic muscle in endothermic vertebrates (Pough et al., 1992; Bevier, 1995; Ressel, 1996; Wells, 2001). Leg muscles tend to be comprised of mostly anaerobic fast glycolytic fibers with

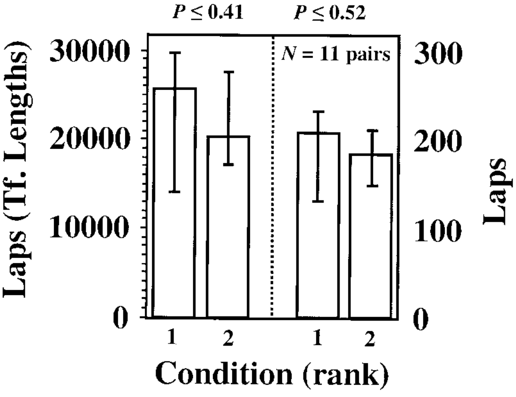

FIG. 5. Swimming distance (medians and interquartile ranges; distance = tibiafibula lengths of the swimmer) of males when members of each pair were ranked by condition (N = 11 pairs). P-levels are for a two-sided Wilcoxon Matched Pairs Signed Rank Test.

enzyme profiles that reflect this difference (Putnam and Bennett, 1983; Marsh and Taigen, 1987; also see Gans and De Dueldre, 1992:288). Leg muscles also have lower mitochondrial and capillary densities, less extensive sarcoplasmic reticula, and smaller quantities of endogenous fuel stores than do calling muscles (Marsh and Taigen, 1987; Pough et al., 1992; Ressel, 2001), although contractile properties tend to be similar (McLister et al., 1995; Marsh, 1999). In spite of the profound differences in the morphological and physiological attributes of muscles associated with locomotion and vocalization, it is not unreasonable to expect a positive correlation between some performance measures during these two forms of activity. This is because, at high activity levels, features related to the supply and delivery of fuel and oxygen to muscles as well as removal of waste products, may constrain muscle activity in different areas in the body. For example, Zimmitti (1999) found that male Spring Peepers that called at above average rates had higher hemoglobin concentrations and greater ventricular masses than males that called at rates below chorus averages. These characteristics of the cardiovascular system may also impact on the performance of locomotory muscles as measurements of oxygen consumption during exercise of some anuran species indicate (Hillman, 1976; Walsberg et al., 1986). However, a cautionary note is warranted. Aerobic capacities are relatively low in the ranids examined in the aforementioned studies, and males are unable to sustain high levels of vocal activity or movement. In the context of the current study species, the contribution of constraints imposed by the central features of cardiovascular and respiratory system may be tenuous because maximal measured metabolic rates during (albeit brief) bouts of forced locomotory exercise are well below those that can be achieved during sustained calling (see Discussion in Marsh and Taigen, 1987). As pointed out by Marsh and Taigen, metabolic limits may reflect the contribution of "both central O_2 delivery and local tissue factors." If local tissue factors (i.e., muscle characteristics) rather than attributes of the cardiovascular and respiratory system predominantly and independently limited swimming and calling in our *H. versicolor*, the significant relationship we found between these performance measures may be coincidental.

Although we have no direct evidence, we believe that pulse effort in Gray Treefrogs better reflects cardiovascular condition than does call duration. The cost of calling, as measured by the rate of oxygen consumption, rises with pulse effort but not call duration (Wells and Taigen, 1986; Grafe, 1997). Moreover, in *H. versicolor*, males change call duration with changes in chorus density or experimental acoustic stimulation in a rapid and reversible fashion (Wells and Taigen, 1986; Schwartz et al., 2002). These changes are typically accompanied by opposing changes in call rate such that pulse effort remains about the same. However, some other constraint may operate on call duration because within choruses on a given night the ranking of males for this attribute tends to be fairly stable during most of an evening, whether or not groups of males are shifting from relatively longer calls to shorter calls (see Schwartz et al., 2002).

Both swimming and calling rely on stored reserves of energy. In *H. versicolor*, in which each pulse produced involves a separate contraction of the trunk musculature (Girgenrath and Marsh, 1997), calling is powered predominantly by intramuscular glycogen and fat. Although these two substrates are used in a ratio of approximately 1:3 (Wells et al., 1995; Grafe, 1997), glycogen probably imposes the more important constraint on the duration of calling activity in an evening (Wells et al., 1995; Schwartz et al., 1995). Wells et al. (1995) reported over a 60% decline in the trunk muscle glycogen of males after 2.0–2.5 h of chorusing. Liver reserves of glycogen probably contribute little during actual calling in Gray Treefrogs but together with food may be used to replenish intramuscular energy stores depleted during vocal activity (Wells et al., 1995; Wells, 2001). During prolonged bouts of locomotion, phosphocreatine is depleted relatively early (Gatten et al., 1992) and leg muscles also rely principally on fat and glycogen to fuel activity with glycogen depletion impacting on performance and ultimately endurance (Gleason, 1991).

In the present study, it is probable that our measures of calling performance did not reflect differences in energetic reserves of males. Indeed, the data from a number of species on this matter are equivocal (Green, 1990; Docherty et al., 1995; Marler and Ryan, 1996). As suggested by Wagner and Hoback (1999) and Tárano (2001), who failed to find a correlation between acoustic signaling and condition in studies of a cricket, *Gryllus lineaticeps*, and a leptodactylid frog, *Physalaemus enesfae*, respectively, part of the explanation may be that males channel more of their excess (i.e., disposable = above that required for basic maintenance) energy reserves into calling. Accordingly, more vocally capable, high-quality males fail to accumulate more substantial fuel stores than do less capable individuals (for discussion of additional complications, see Dyson et al., 1998; McLister, 2003). If this were so, it would explain the lack of significant relationships between condition and call duration or pulse effort that we observed. Additionally, the effect of a male's recent feeding history and condition on calling performance may be subtle or manifest only when energy reserves are nearly exhausted and so very difficult to detect in a sample of males whose energetic reserves have not been experimentally manipulated. For example, Schwartz et al. (1995) found that in *H. microcephala* note rate was not correlated with trunk muscle glycogen reserves measured at the end of an evening of calling, suggesting that male calling declines sharply only as glycogen reserves near depletion (Schwartz et al., 1995). J. J. Schwartz and B. W. Buchanan (unpubl. data) found that unfed male *H. versicolor* males showed only a dramatic decline in calling performance on their final (fifth) night of calling in an enclosed pond.

Because calling of Gray Treefrogs was monitored for just 30 min in the current study, and males continued to call afterward, it seems certain that exhaustion did not contribute to differences in vocal behavior of our subjects. However, although we found no relationship between our condition measure and swimming endurance, some of our swimming trials lasted over two hours and, thus, it seems likely that energetic reserves did impact on the distances that males swam. Anaerobic as well as aerobic metabolism power locomotion in anurans and so lactate accumulation (Taigen and Beuchat, 1984; Gleason, 1991; Gatten et al., 1992) as well as fuel depletion probably contributed to exhaustion in our subjects. For example, in African Clawed Frogs, *Xenopus laevis*, forced to rapidly swim 51.5 m, levels of muscle glycogen dropped by nearly 75% while lactate levels more than tripled (Miller and Camilliere, 1981). However, in our study, males were allowed to choose their own swimming speed, and we cannot be certain of the degree, if at all, to which subjects exceeded their maximum aerobic speed. Nevertheless, a male with a cardiovascular and respiratory system better able to meet the demands of our prolonged forced exercise test, which could last over two hours, would better able to minimize the hypoxia contributing to elevated intramuscular lactate.

An especially curious finding was that the males that gave the longer calls swam less than the males that gave the shorter calls. In fact, positive correlations between performance measures during different forms of exercise (and even within the general category of locomotion) may be lacking in amphibians (Navas et al., 1999). As suggested above, the two measures of vocal performance we considered may be subject to different morphological and physiological constraints rendering their mutual concordance with performance during other forms of exercise unlikely. In addition, motivational factors may obscure relationships. For example, in a study that examined relationships between a number of naturally occurring behaviors (calling, searching, clasping) of American Toads (*Bufo americanus*) in a chorus, Wells and Taigen (1984) noted agreement between different forms of activity such that some males were consistently more active than others. However, they failed to find a correlation between an approximation of calling effort in the field and aerobic capacity during forced exercise. A suggested explanation was that some males were vocalizing at submaximal levels. In our treefrogs, although our swimming tests probably pushed individuals to their limit of endurance, it is likely that males were not using calls as long as they were capable of producing. However, this would not explain the unexpected yet significant relationship we found. Our results, therefore, may reflect some unknown trade-off between call duration and the capacity for prolonged locomotory exercise that must await future study.

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LITERATURE CITED

BEVIER, C. R. 1995. Biochemical correlates of calling activity in Neotropical frogs. Physiological Zoology 68:1118–1142.

DOCHERTY, S., P. J. BISHOP, AND N. I. PASSMORE. 1995. Calling behavior and male condition in the frog *Hyperolius marmoratus*. Journal of Herpetology 29:616–618.

DOTY, G. V., AND A. M. WELCH. 2001. Advertisement call duration indicates good genes for offspring feeding rate in Gray Tree Frogs (*Hyla versicolor*). Behavioral Ecology and Sociobiology 49:150–156.

DYSON, M. L., S. P. HENZI, T. R. HALLIDAY, AND L. BARRETT. 1998. Success breeds success in mating male Reed Frogs (*Hyperolius marmoratus*). Proceedings of the Royal Society London B, Biological Sciences 265:1417–1421.

GANS, C., AND G. DE GUELDRE. 1992. Striated muscle: physiology and functional morphology. *In* M. E. Feder and W. W. Burggren (eds.), Environmental Physiology of the Amphibians, pp. 277–313. University of Chicago Press, Chicago.

GATTEN JR., R. E., K. MILLER, AND R. J. FULL. 1992. Energetics at rest and during locomotion. *In* M. E. Feder and W. W. Burggren (eds.), Environmental Physiology of the Amphibians, pp. 314–377. University of Chicago Press, Chicago.

GERHARDT, H. C. 1994. The evolution of vocalization in frogs and toads. Annual Review of Ecology and Systematics 25:293–324.

GERHARDT, H. C., M. L. DYSON, AND S. D. TANNER. 1996. Dynamic properties of the advertisement calls of Gray Tree Frogs: patterns of variability and female choice. Behavioral Ecology 7:7–18.

GIRGENRATH, M., AND R. L. MARSH. 1997. In vivo performance of trunk muscles in tree frogs during calling. Journal of Experimental Biology 200: 3101–3108.

———. 2003. Season and testosterone affect contractile properties of fast calling muscles in the Gray Tree Frog *Hyla chrysoscelis*. American Journal of Physiology—Regulatory, Integrative and Comparative Physiology 284:R1513–R1520.

GLEASON, T. T. 1991. Patterns of metabolic recovery from exercise in amphibians and reptiles. Journal of Experimental Biology 160:187–207.

GRAFE, T. U. 1997. Use of metabolic substrates in the Gray Treefrog *Hyla versicolor*: implications for calling behavior. Copeia 1997:356–362.

GRAFE, T. U., AND J. THIEN. 2001. Energetics of calling and substrate use during prolonged exercise in the European Treefrog, *Hyla arborea*. Journal of Comparative Physiology B. 171:69–76.

GREEN, A. J. 1990. Determinants of chorus participation and the effects of size, weight and competition on advertisement calling in the Tungara Frog, *Physalaemus pustulosus* (Leptodactylidae). Animal Behaviour 39:620–638.

HILLMAN, S. S. 1976. Cardiovascular correlates of maximal oxygen consumption rates in anuran amphibians. Journal of Comparative Physiology 109B:199–207.

KLUMP, G. M., AND H. C. GERHARDT. 1987. Use of non-arbitrary acoustic criteria in mate choice by female Gray Treefrogs. Nature 326:286–288.

MARLER, C. A., AND M. J. RYAN. 1996. Energetic constraints and steroid hormone correlates of male calling behaviour in the Túngara Frog. Journal of Zoology 240:397–409.

MARSH, R. L. 1999. Contractile properties of muscles used in sound production and locomotion in two species of Gray Tree Frog. Journal of Experimental Biology 202:3215–3223.

MARSH, R. L., AND T. L. TAIGEN. 1987. Properties enhancing aerobic capacity of calling muscles of Gray Tree Frogs *Hyla versicolor.* American Journal of Physiology 252:R7786–R7793.

MCLISTER, J. D. 2003. The metabolic cost of amplexus in the Grey Tree Frog (*Hyla versicolor*): assessing the energetics of male mating success. Canadian Journal of Zoology 81:388–394.

MCLISTER, J. D., E. D. STEVENS, AND J. P. BOGART. 1995. Comparative contractile dynamics of calling and locomotor muscles in three hylid frogs. Journal of Experimental Biology 198:1527–1538.

MILLER, K., AND J. H. CAMILLIERE. 1981. Physical training improves swimming performance of the African Clawed Frog *Xenopus laevis*. Herpetologica 37: 1–10.

MURPHY, C. G. 1994. Determinants of chorus tenure in the Barking Treefrogs (*Hyla gratiosa*). Behavioral Ecology and Sociobiology 34:285–295.

NAVAS, C. A., R. S. JAMES, J. M. WAKELING, K. M. KEMP, AND I. A. JOHNSTON. 1999. An integrative study of the temperature dependence of whole animal and muscle performance during jumping and swimming in the frog *Rana temporaria*. Journal of Comparative Physiology B 169:588–596.

POUGH, F. H., W. E. MAGNUSSON, M. J. RYAN, K. D. WELLS, AND T. L. TAIGEN. 1992. Behavioral energetics. *In* M. E. Feder and W. W. Burggren (eds.), Environmental Physiology of the Amphibians, pp. 395–436. University of Chicago Press, Chicago.

PRESTWICH, K. N. 1994. The energetics of acoustic signaling in anurans and insects. American Zoologist 34:625–643.

PUTNAM, R. W., AND A. F. BENNETT. 1983. Histochemical, enzymatic, and contractile properties of skeletal muscles of three anuran amphibians. American Journal of Physiology 244:R558–R567.

RESSEL, S. J. 1996. Ultrastructural properties of muscles used for call production in Neotropical frogs. Physiological Zoology 69:952–973.

———. 2001. Ultrastructural design of anuran muscles used for call production in relation to the thermal environment of a species. Journal of Experimental Biology 204:1445–1457.

ROME, L. C., E. D. STEVENS, AND H. B. JOHN-ALDER. 1992. The influence of temperature and thermal acclimation on physiological function. *In* M. E. Feder and W. W. Burggren (eds.), Environmental Physiology of the Amphibians, pp. 183–205. University of Chicago Press, Chicago.

RUNKLE, L. S., K. D. WELLS, C. C. ROBB, AND S. L. LANCE. 1994. Individual, nightly, and seasonal variation in calling behavior of the Gray Treefrog, *Hyla versicolor*: implications for energy expenditure. Behavioral Ecology 5:318–325.

RYAN, M. J. 1988. Energy, calling, and selection. American Zoologist 28:885–898.

SCHWARTZ, J. J. 1993. Male calling behavior, female discrimination and acoustic interference in the Neotropical Treefrog *Hyla microcephala* under realistic acoustic conditions. Behavioral Ecology and Sociobiology 32:401–414.

———. 2001. Call monitoring and interactive playback systems in the study of acoustic interactions among male anurans. *In* M. J. Ryan (ed.), Anuran Communication, pp. 183–204. Smithsonian Institution Press, Washington, DC.

SCHWARTZ, J. J., S. RESSEL, AND C. R. BEVIER. 1995. Carbohydate and calling: depletion of muscle glycogen and the chorusing dynamics of the Neotropical Treefrog *Hyla microcephala*. Behavioral Ecology and Sociobiology 37:125–135.

SCHWARTZ, J. J., B. W. BUCHANAN, AND H. C. GERHARDT. 2001. Female mate choice in the Gray Treefrog (*Hyla versicolor*) in three experimental environments. Behavioral Ecology and Sociobiology 49: 443–455.

———. 2002. Acoustic interactions among male Gray Treefrogs (*Hyla versicolor*) in a chorus setting. Behavioral Ecology and Sociobiology 53:9–19.

SULLIVAN, B. K., AND S. H. HINSHAW. 1992. Female choice and selection on male calling behaviour in the Grey Treefrog *Hyla versicolor.* Animal Behaviour 44:733–744.

SULLIVAN, B. K., M. J. RYAN, AND P. A. VERRELL. 1995. Female choice and mating system structure. *In* H. Heatwole and B. K. Sullivan (eds.), Amphibian Biology. Vol 2. Social Behaviour, pp. 496–517.

Chipping Norton, Surrey Beatty and Sons, New South Wales, Australia.

TAIGEN, T. L, AND C. A. BEUCHAT. 1984. Anaerobic threshold of anuran amphibians. Physiological Zoology 57:641–647.

TAIGEN, T. L., K. D. WELLS, AND R. L. MARSH. 1985. The enzymatic basis of high metabolic rates in calling frogs. Physiological Zoology 58:719–726.

TÁRANO, Z. 2001. Variation in male advertisement calls in the Neotropical Frog *Physalaemus enesefae*. Copeia 2001:1064–1072.

WAGNER JR., W. E., AND W. W. HOBACK. 1999 Nutritional effects on male calling behavior in the variable field cricket. Animal Behaviour 57:89–95.

WALSBERG, G. E., M. S. LEA, AND S. S. HILMAN. 1986. Individual variation in maximum aerobic capacity: cardiovascular and enzymatic correlates in *Rana catesbeiana*. Journal of Experimental Zoology 239: 1–5.

WELCH, A. M. 2003. Genetic benefits of a female mating preference in Gray Tree Frogs are context dependent. Evolution 57:883–893.

WELCH, A. M., R. L. SEMLITSCH, AND H. C. GERHARDT. 1998. Call duration as a reliable indicator of ''good genes'' in the Gray Treefrog. Science 280:1928–1930.

WELLS, K. D. 1988. The effects of social interactions on anuran vocal behavior. *In* B. Fritzsch, W. Wilczynski, M. J. Ryan, T. Hetherington, and W. Walkowiak (eds.), The Evolution of the Amphibian Auditory System, pp. 433–454. John Wiley, New York.

———. 2001. The energetics of calling in frogs. *In* M. J. Ryan (ed.), Anuran Communication, pp. 45–60. Smithsonian Institution Press, Washington, DC.

WELLS, K. D., AND T. L. TAIGEN. 1984. Reproductive behavior and aerobic capacities of male American Toads (*Bufo americanus*): is behavior constrained by physiology? Herpetologica 40:292–298.

———. 1986. The effect of social interactions on calling energetics in the Gray Treefrog (*Hyla versicolor*) Behavioral Ecology Sociobiology 19:9–18.

WELLS, K. D., T. L. TAIGEN, S. W. RUSCH, AND C. C. ROBB. 1995. Seasonal and nightly variation in glycogen reserves of calling Gray Treefrogs (*Hyla versicolor*). Herpetologica 51:359–368.

ZIMMITTI, S. J. 1999. Individual variation in morphological, physiological, and biochemical features associated with calling in Spring Peepers (*Pseudacris crucifer*). Physiological and Biochemical Zoology 72:666–676.

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Social Interactions in *Hypsiboas albomarginatus* (Anura: Hylidae) and the Significance of Acoustic and Visual Signals

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ABSTRACT.—**Social behavior of *Hypsiboas albomarginatus* was studied in the Atlantic rain forest, Municipality of Ubatuba, in the north coast of the State of São Paulo, southeastern Brazil. Vocalizations of *H. albomarginatus* are described, including contexts in which they were emitted and temporal and spectral parameters differentiating advertisement from aggressive calls. Dominant call frequency was inversely correlated with male length and body mass but not with environmental temperature. Number of pulses per note was not correlated with any variable, and advertisement call amplitude was influenced by temperature and time. During chorus aggregation, males interacted acoustically by emitting advertisement calls in antiphony, or by emitting aggressive calls. Some disputes among males culminated in physical combat; males performed kicks and slaps on rivals' heads, in an apparent attempt to dislodge rivals from perches. Visual signals were also displayed during conflicts between males, contributing to an escalation of aggressive behavior. Visual signals were not recorded during courtship between males and females but may help in the accurate localization of the signaling male during aggressive interactions.**

Most anuran aggregations are formed during the reproductive period, when males emit calls to attract females (Duellman and Trueb, 1986). Most anuran social behavior involves disputes among males for access to females (Wells, 1977). Conflicts in this process are typically resolved through emission of aggressive calls (Cardoso and Haddad, 1984; Bastos and Haddad, 1995; Martins et al., 1998) and visual displays, involving colored or contrasting body parts (Wells,

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