Journal of Herpetology, Vol. 45, No. 1, pp. 45–49, 2011

Acoustic Communication in the Kihansi Spray Toad (*Nectophrynoides asperginis*): Insights from a Captive Population

Victoria S. Arch,[1,2] Corinne L. Richards-Zawaki,[3] and Albert S. Feng[4]

[1]*Department of Biology, Stanford University, Stanford, California 94305 USA; E-mail: varch@stanford.edu*
[3]*Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana 70118 USA*
[4]*Department of Molecular and Integrative Physiology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801 USA*

Abstract.—**Acoustic signals play an important role in intraspecific communication for most anurans. We investigated the vocal signals, communication, and ear morphology of captive Kihansi Spray Toads (*Nectophrynoides asperginis*), an Extinct in the Wild diurnal species that is endemic to a specialized spray zone created by waterfalls of the Kihansi River Gorge in Tanzania. We found that *N. asperginis* have reduced ears, and their calls are soft and simple, comprising short call notes with a fundamental frequency of ∼4.1 kHz and harmonics extending into the ultrasonic range. Observations of the toads' interactions while calling indicate that males call primarily when they are in visual contact or behaviorally engaged with a conspecific. These observations suggest that social interactions in Spray Toads likely involve multimodal sensory communication. *Nectophrynoides asperginis* has apparently adapted to communicate amid high-level ambient noise produced by the waterfalls in its native environment by specializing in short-range communication within high-density aggregations.**

Sound communication plays a key role in the reproduction of most anurans. For the majority of species, females use the acoustic signals of males to discriminate between conspecifics and heterospecifics (reviewed in Wells, 2007; Gerhardt and Huber, 2002; Blair, 1963, 1964, 1968) and to locate mates. Therefore for acoustically communicating frogs and toads, the effective transmission of vocalizations between signaler and receiver is vital to fitness. Amphibian populations are declining worldwide because of multiple factors, including habitat loss, climate change, and disease (Stuart et al., 2004). As species go extinct in the wild, captive populations are being maintained in zoos and protected areas in the hope of eventual reestablishment in native, or comparable, habitats. Characterizing the call repertoire of endangered species, and observing the social contexts in which calls are produced, could inform management strategies for sustaining viable captive populations and for reestablishment.

The Kihansi Spray Toad (*Nectophrynoides asperginis*) is a critically endangered toad in the family Bufonidae and is endemic to small patches of unique wetlands generated by waterfalls in the Kihansi River Gorge of the Udzungwa Mountains of Tanzania (Poynton et al., 1998). The main falls are 100 m high and plunge into a pool surrounded by steep rock walls, generating large quantities of spray. This spray creates a specialized, humid microenvironment on which the toads rely (Poynton et al., 1998). *Nectophrynoides asperginis* appears to have one of the smallest (∼2 ha, Poynton et al., 1998) native ranges of any amphibian. Since the diversion of the Kihansi River for a major hydroelectric project in 1999, the Kihansi Spray Toad is believed to be Extinct in the Wild and remains only in captive populations in zoos. Reintroduction strategies for this species are being discussed and would benefit from consideration of the toads' acoustic sensory ecology, which is hitherto unexplored.

The present study characterizes the vocal repertoire of *N. asperginis*, including an examination of the variability of its calls in different social contexts. Although calling has previously been noted during male–male agonistic interactions and courtship (CLR, unpubl. obs.), it is not known whether or how vocal signals under these contexts differ. In addition, visual inspection of the toads revealed that there is no external tympanum; thus the toads appear to be ''earless'' (Fig. 1; Jaslow et al., 1988). We examined the morphology of the species' peripheral auditory system to investigate the anatomical substrates of sound reception. Our goal was to augment current understanding of the toads' natural behavior by describing key components of their sonic communication system.

[2]Corresponding Author.

Materials and Methods

Studies of *N. asperginis* were conducted in August 2006 at the Toledo Zoo in Toledo, Ohio, with permission from the Tanzanian government's Lower Kihansi Environmental Management Project (LKEMP). This research was performed under the guidelines established by the Toledo Zoo and the University of Illinois' Institutional Animal Care and Use Committee (IACUC, permit 04133).

We made acoustic recordings of Spray Toad vocalizations from 6–10 August 2006 between 0900 and 1700 h at the Toledo Zoo. We placed the toads in a plastic mesh cage (15 × 20 × 25 cm; L × W × H), provided them with an ample substrate of moss and small plants and misted them frequently to prevent desiccation. The toads were arranged in three different social conditions: (1) a single male and female; (2) three males and no females; (3) two males and a single female. Different individuals were used in each treatment, and the treatments were unreplicated. Males and females are sexually dimorphic in body size and coloration (Fig. 1); the females are considerably larger, and the males have dark inguinal patches, thus the two sexes are easily distinguishable. The different social groupings allowed us to observe male–male as well as male–female behavioral interactions. The toads' spontaneous calls were recorded using a custom-built PC-based recording device (PC-Tape) and a custom-made directional microphone with a flat frequency response from 15–120 kHz and a roll-off of 10 dB/octave and 6 dB/octave at <15 kHz and >120 kHz, respectively (Narins et al., 2004; Feng et al., 2006). The microphone was placed approximately 10 cm above the calling toad(s). Signals were digitized using a 16-bit A/D converter at a sampling rate of 96–256 kHz, with 8× oversampling. Higher sampling rates were used to examine in detail the full spectrum of the calls, including ultrasonic spectral components (see below). Lower sampling rates were used during longer recording periods to reduce file size. Data were saved as WAV files and analyzed (1,024 points fast Fourier transform) and displayed using SELENA, a custom-designed program. Observer comments were recorded with a separate microphone, which was fitted with a switch to allow remote control of PC-Tape. Toad behavior while calling was monitored visually. If the toads were not interacting physically, we subjectively determined whether they were in visual contact by

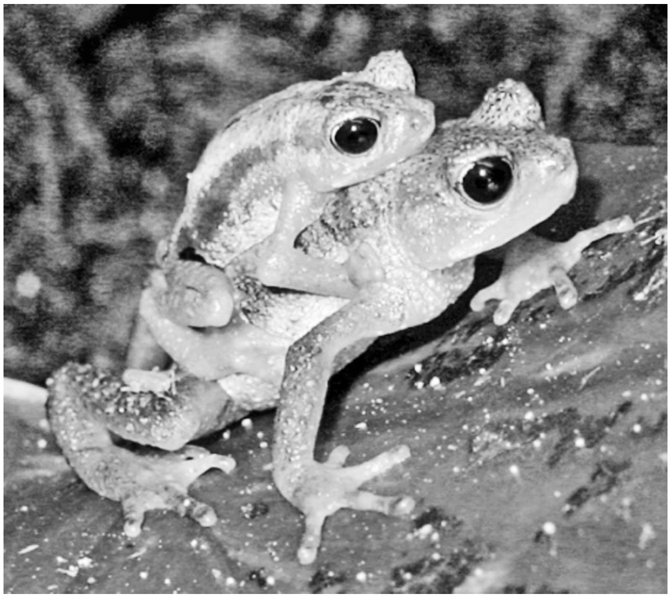

FIG. 1. Photograph of male (top) and female (bottom) Spray Toads in amplexus. Note that tympana are not distinguishable in either sex.

observing whether they were facing each other, and the intervening space was free of obstructions. The absolute sound pressure levels of the vocalizations were determined with a portable sound level meter (Brüel and Kjaer model 2239) set to measure RMS SPL and positioned approximately 8–12 cm from the calling toad.

Nectophrynoides asperginis calls are typically emitted in bouts of 2–7 individual pulses, or notes. Therefore, to characterize the calls of *N. asperginis*, we measured: (1) the duration (in sec.) of individual call notes; (2) the interval between successive call notes (i.e., internote interval) within a bout; (3) the interval between bouts (i.e., interbout interval); and (4) the fundamental (and in this case the dominant) frequency of the notes. These parameters, as well as the calling rate per minute, were averaged and compared among four individual males (38–76 calls or bouts per male). We also compared the call parameters of these males among the different social contexts in which they were emitted. For example, calls given while monitoring, approaching, or wrestling with another male (averaged over 136–140 calls/bouts) were compared to those given while monitoring or approaching a female (averaged over 66 to 75 calls/bouts).

Ear Morphology.—To characterize the morphology of the *N. asperginis* peripheral auditory system, an adult male, which had died of natural causes and was preserved in formalin, was examined histologically. The specimen was decapitated and the head embedded in paraffin and sectioned (6 µm) in the transverse plane. The sections were stained with hematoxylin–eosin and viewed under a light microscope and photographed at 20–100× power.

RESULTS

Calling Behavior.—We observed numerous social interactions between the *N. asperginis* individuals. Aggressive encounters were frequent between males in treatments (2) and (3). During such encounters, a dominant male was typically easy to identify because he assumed a threat posture, characterized by full extension of the forearms, and produced bouts of vocalizations. In response, the subordinate male either retreated or engaged in vocal duets; in the latter case, the aggressive male typically initiated physical combat (i.e., wrestling). While wrestling, both males usually continued vocalizing until there was a decisive victor. Sighting of a female during courtship encounters similarly triggered male vocalization, which was often accompanied by approach and pursuit of the female.

Males seldom vocalized when they were isolated (i.e., not in visual contact or not interacting with a conspecific at short range). For example, when three males were housed in the test cage but not in visual contact, the collective calling rate was 3.1 calls/min over a period of 30+ min. In contrast, these males' calling rate during social encounters was 30.8 calls/min over a period of 6.5 minutes; the result from the group of two males and one female was similar (31.4 calls/min in social encounters in 6+ min). These results indicate that the toads' social interactions involve acoustic signaling.

Call Structure and Variation.—The vocalizations of *N. asperginis* comprise brief call notes (or tone pulses), given either in isolation (Fig. 2A), or more commonly in bouts of 2–7 call notes at a constant internote interval (Fig. 2B–D). The duration of call notes averages 37.4 ms; the average internote interval within a bout is 85 ms, and the interbout interval averages 930.7 ms (Table 1). The fundamental frequency (F0), which is also the dominant frequency, is 4,071 Hz (Table 1). Most calls contain multiple harmonics with some harmonics reaching well into the ultrasonic range (up to 40 kHz; Fig. 2). The second harmonic is on average 25–30 dB lower in amplitude than the fundamental frequency. The half-width of the F0 (the bandwidth at 6 dB below the peak energy at F0) averages 783 ± 131 Hz. Call notes are generally soft, with an RMS sound pressure level of 69–72 dB SPL (re: 20 µPa), at a distance of ~10 cm. When calls directed at females (courtship) and those directed at males (aggressive) were compared for two males, we found that the aggressive calls tend to have a shorter average duration (36.7 vs. 42.5 ms), longer internote interval (83.4 vs. 71.9 ms), longer interbout interval (920.5 vs. 817.6 ms), and lower fundamental frequency (4,103 vs. 4,146 Hz) than the courtship calls. However, the small sample size prohibits these differences from being tested statistically.

Ear Morphology.—Serial cross-sections of the peripheral auditory system reveal that the toads do not have an air-filled middle ear and their inner ear is not connected to any structure on the body surface. The inner ear of *N. asperginis* has a distinct operculum (Fig. 3C, D) and a stapes (Fig. 3E, F) abutting the oval window; the operculum is attached to the opercularis muscle (Fig. 3C, D) whose caudal end is anchored to the dorsal tip of the suprascapular cartilage (Fig. 3A). Given the morphological characteristics of the inner ear, its stimulation likely involves sound transmission from the lung to the mouth cavity and then to the eustachian tube (Fig. 3H) and the operculum. This stimulation mode resembles the pathway hypothesized for toads of the genus *Atelopus* and the fire-bellied toad (*Bombina bombina*), involving the respiratory passages, pharynx and mouth cavity (Lindquist et al. 1998; Hetherington and Lindquist 1999).

DISCUSSION

In the present study, we characterized the acoustic communication system of the Kihansi Spray Toad in captivity. Although our studies are limited to laboratory observations (as they could not be realized in the wild), and have small sample sizes caused by the toads' protected status, we believe that they provide useful insight into the communication behavior of this threatened species.

Waterfalls are a source of high-level, broadband ambient noise that has the potential to mask intraspecific acoustic signals. In fact, the presence of noise, both abiotic (e.g., wind, flowing water) and biotic (e.g., the calls of conspecific or heterospecific males), has been shown to affect the ability of female anurans to detect and discriminate among male calls (Schwartz and Gerhardt, 1998; Wells and Schwartz, 2006). As a result, many species have evolved physiological and behav-

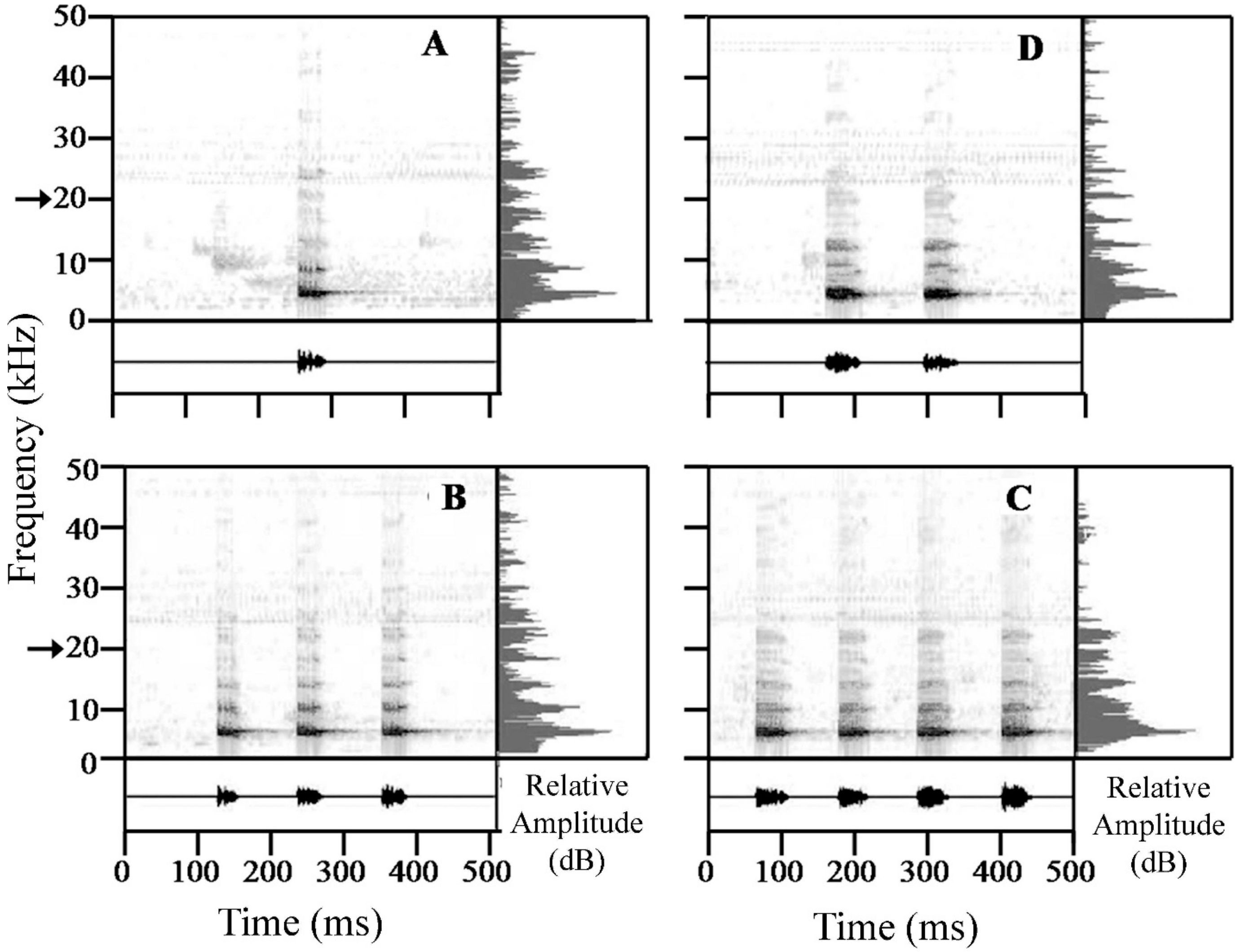

FIG. 2. Sound spectrogram (top left panel), waveform (bottom panel), and instantaneous amplitude spectrum (right panel) of representative vocal signals of a male *Nectophrynoides asperginis*. Shown are a one note call (A), a bout of two notes (B), a bout of three notes (C), and a bout of four notes (D). The continuous high-frequency bands (e.g., around 25–30 kHz and 45–50 kHz) were produced by ambient background noise during the recording sessions. Arrows denote the boundary between audible and ultrasonic frequencies.

ioral mechanisms to minimize the impact of environmental noise on the transmission and reception of their calls. Although recordings of the ambient noise generated by the waterfalls of the Kihansi River Gorge are not available, researchers conducting bird surveys in the gorge noted that the falls are loud enough to prohibit auditory bird censuses (Cordiero et al., 2006). The broadband noise spectrum produced by a montane waterfall is presented in figure 2b in Feng et al. (2006). Given the 100-m height of the main Kihansi falls, we hypothesize that the ambient noise levels produced by these falls is equivalent to, or greater than, those of the waterfalls presented by Feng and colleagues. Thus, it is likely that persistent, high-level background noise has played a selective role in shaping the acoustic communication strategies employed by the Spray Toads.

Short-Range Communication in Nectophrynoides asperginis.—Predecline surveys of the Kihansi River Gorge found the Spray Toads in extremely high densities. In fact, the estimate of 4.27 per m^2 (Poynton et al., 1998) is the second highest density ever documented for an anuran species, and this number was considered a conservative estimate because the toads were extremely difficult to find in the dense vegetation. Several lines of evidence from our observations suggest that the vocal behavior of *N. asperginis* is best suited for short-range communication within such dense aggregations. First, it is well established that the temporal and spectral characteristics of animal vocal signals are subject to distortion during sound transmission (reviewed in Michelsen, 1978; Wiley and Richards, 1978; Forrest, 1994; Bradbury and Vehrencamp, 1998;

TABLE 1. Temporal and spectral parameters of the call notes of male *N. asperginis*.

Call parameter	*N* total # analyzed calls (# per ind.)	Mean	SD	Minimum	Maximum
Note duration (ms)	226 (50,50,51,75)	37.4	13.3	5.6	75.0
Internote interval (ms)	226 (50,50,51,75)	85.0	12.1	58.0	143.0
Interbout interval (ms)	206 (50,39,51,66)	930.7	266.1	288.0	2076.0
Fundamental frequency (Hz)	230 (50,50,53,77)	4071	165	3576	4494

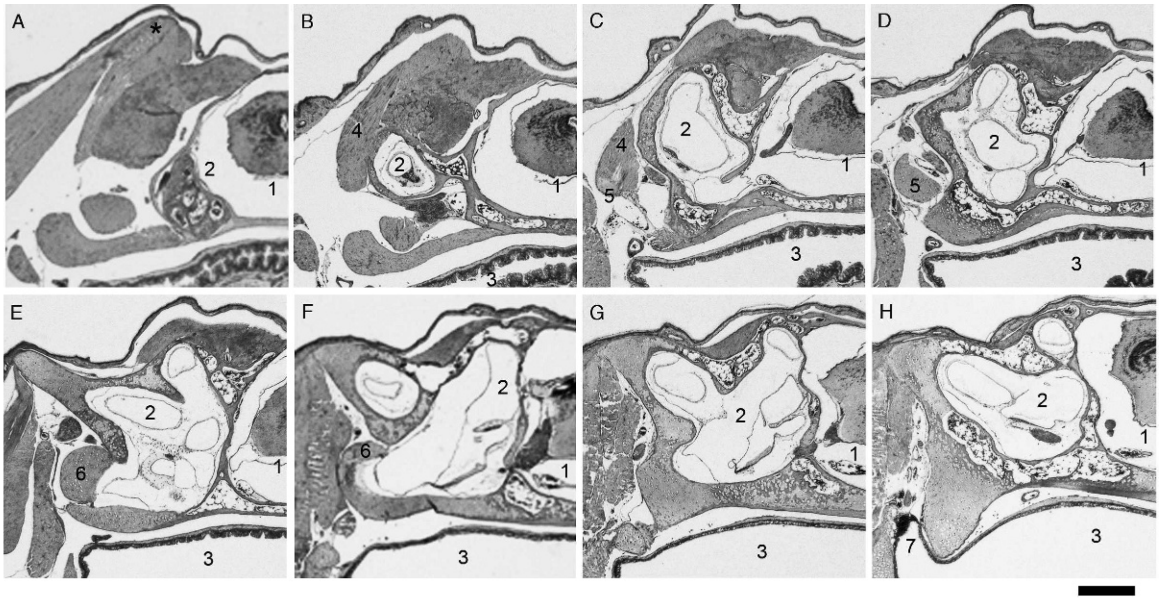

FIG. 3. Transverse histological sections (6-µm thick, hematoxylin and eosin stain) of the Spray Toad's inner ear (structure 2 in Panels A–H) showing the stapes (structure 6 in Panels E and F), plus the operculum (structure 5 in Panels C and D) as well as its attachment to the opercularis muscle (structure 4 in Panels B and C); this muscle is anchored to the scapular cartilage caudally (* in Panel A). Structures 1 and 3 in Panels A–H refer to the toad's brain and mouth cavity, respectively; structure 7 in Panel H refers to the toad's left eustachian tube. Panel A is the caudal-most section. Panels A through H progresses rostrally, and these are 96, 48, 24, 48, 24, 72, and 48 µm apart. Calibration bar is 500 µm.

Padgham, 2004). High frequencies are more severely attenuated with distance but are more easily localizable than low frequencies (Wiley and Richards, 1978; Feng and Schul, 2006). Thus, the soft, high-frequency calls of *N. asperginis* are suited for short-range mate attraction and territorial defense. Second, *N. asperginis* is a diurnal species, and our observations suggest that visual contact with another toad (male or female) elicits males to call, much like the induction of agonistic behavior in a diurnal Dart-Poison Frog (Narins et al., 2003, 2005). Such a multimodal communication system in a densely vegetated habitat would necessarily limit intraspecific communication to the short range over which visual contact can be established. Finally, *N. asperginis* is an earless species, possessing a typical anuran inner ear but lacking a tympanic membrane and air-filled middle ear cavity (Figs. 1, 3). Earless anurans are sensitive to airborne sound; however, these species must rely on extratympanic sound transmission routes, which are generally less effective than tympanic transmission of frequencies above 1,000 Hz (Jaslow et al., 1988; Mason, 2006). Because of their protected status, we did not test the toads' hearing sensitivity electrophysiologically; however, we speculate that their hearing sensitivity is reduced in comparison to anurans with tympanic ears, in accord with other earless species.

Taken together, the presumed reduced auditory sensitivity of *N. asperginis* and their soft, high-frequency vocal output suggest the toads' acoustic communication is restricted to short ranges. Validation of this hypothesis will require further research to establish the species' full hearing range and sensitivity, perhaps using a noninvasive procedure such as measuring the auditory brainstem response.

Ultrasonic Communication.—Behavioral and neurophysiological experiments recently demonstrated that two frog species, *Odorrana tormota* and *Huia cavitympanum*, use ultrasonic harmonics of their calls (*O. tormota*) or purely ultrasonic calls (*H. cavitympanum*), for intraspecific communication (Feng et al., 2006; Arch et al., 2009). Both species breed alongside rushing mountain streams and waterfalls that produce substantial background noise. It has been hypothesized that these frogs shifted to a high-frequency communication channel to bypass the broadband but predominately low-frequency ambient noise in their habitats (Narins et al., 2004; Feng et al., 2006; Arch et al., 2009). The ability of these frogs to produce and detect ultrasound provides a compelling example of how anuran communication systems can evolve to meet the challenges of sending and receiving acoustic signals in noisy environments.

It is likely that the waterfalls of the Kihansi River Gorge produce intense broadband noise with maximum energy at low frequencies, similar to the ambient noise in the habitats of *O. tormota* and *H. cavitympanum* (Feng et al., 2006; Arch et al., 2009) and other areas featuring large waterfalls (Iyer and Hitchcock, 1974; Tuttle and Ryan, 1982). Thus, *N. asperginis*, *O. tormota*, and *H. cavitympanum* have been subjected to comparable acoustic selection pressure by their noisy environments. Like *O. tormota* and *H. cavitympanum*, the calls of the Kihansi Spray Toad contain spectral energy in the ultrasonic range, which suggests that these species may have converged on the use of ultrasonic communication to avoid ambient acoustic interference. However, the auditory peripheries of the species, are dramatically different: the Kihansi Spray Toad is earless, whereas *O. tormota* and *H. cavitympanum* ears are unusually complex for anurans, with tympanic membranes recessed at the base of chambers in the side of the skull (Feng et al., 2006; Arch et al., 2008). Additional experiments will be required to determine whether *N. asperginis* uses its ultrasonic signal components for intraspecific communication. If future research demonstrates that *N. asperginis* communicates ultrasonically, this species, *O. tormota*, and *H. cavitympanum* will represent an intriguing comparative system in which to study unique peripheral auditory morphological and physiological mechanisms that subserve ultrasonic sensitivity in lower vertebrates.

Conclusion and Management Implications.—Our data on the acoustic communication system of *N. asperginis* suggest this diurnal species has dealt with the challenge of sending and receiving acoustic signals in an extremely noisy habitat by forming high density aggregations within which they communicate via a combination of visual and high-frequency acoustic signals, both of which are unlikely to be seriously affected by the presence of the falls at short range. This preliminary assessment suggests that reintroduction strategies for this Extinct in the Wild species may benefit from focusing on seeding relatively small areas with a high number of individuals, thus ensuring that the toads maintain frequent visual and acoustic contact with conspecifics.

Acknowledgments.—We are grateful to A. Odum, T. Herman, and the Toledo Zoo and also to K. Zippel and the Detroit Zoo for their assistance with this research. We thank the Tanzanian government's Lower Kihansi Environmental Management Project (LKEMP) for the permission to study the Kihansi Spray Toad. This research is supported in part by grants from the National Institutes for Health National Institute for Deafness and Other Communication Disorders (R01DC04998 and R01DC00222). This project was performed in compliance with the Animal Care guidelines of the Toledo Zoo and the University of Illinois' Institutional Animal Care and Use Committee (IACUC, permit 04133). Permission to study *N. asperginis* was granted by LKEMP, and all required state and federal permits have been obtained.

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Accepted: 5 July 2010.