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TORNIERI (ANURA: BUFONIDAE) IN THE AMANI NATURE
RESERVE, TANZANIA

IRIS STARNBERGER¹, PEPIJN KAMMINGA², VICTOR CHIK FOSAH³, AND CLIVE NUTTMAN^{4,5}

¹*Department of Evolutionary Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria*

²*Institute of Biology, University of Leiden, Sylviusweg 72, 2300 RA Leiden, The Netherlands*

³*Department of Geology and Environmental Science, University of Buea, PO Box 63, South West Province,
Buea, Cameroon*

⁴*Tropical Biology Association, Department of Zoology, Downing Street, Cambridge CB2 3EJ, United Kingdom*

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THE 'PUSH-UP' AS A CALLING POSTURE IN *NECTOPHRYNOIDES TORNIERI* (ANURA: BUFONIDAE) IN THE AMANI NATURE RESERVE, TANZANIA

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¹Department of Evolutionary Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

²Institute of Biology, University of Leiden, Sylviusweg 72, 2300 RA Leiden, The Netherlands

³Department of Geology and Environmental Science, University of Buea, PO Box 63, South West Province, Buea, Cameroon

⁴Tropical Biology Association, Department of Zoology, Downing Street, Cambridge CB2 3EJ, United Kingdom

ABSTRACT: Males of Tornier's Forest Toad, *Nectophrynoides tornieri*, were observed to perform a peculiar display posture, the 'push-up': the males raised themselves from a substrate (always a plant structure) by first stretching their fore legs into a 'sit-up' and then their hind legs to assume the position. We examined possible functions for the push-up position in manipulative behavioral experiments. In a majority of the tested males, the introduction of a conspecific male only evoked the less conspicuous sit-up display, whereas a playback of male vocalization more often triggered the full push-up position, usually followed by a vocal response. We found no association between the sit-up and the push-up display and the presence of a female *N. tornieri* near a male's calling perch. Our findings support the hypothesis that the push-up posture is a display in response to other calling males; whilst being the usual calling posture, it might also be important in visual communication. We describe in detail the characteristics of the call for the first time; vocalizing males were found at more elevated positions than previously reported and there were no common distinctive microhabitat features between calling sites.

Key words: Behavior; Bufonidae; Manipulative experiments; *Nectophrynoides tornieri*; Playback; Push-up; Territorial display; Visual communication; Vocalization

IN AMPHIBIANS, signals have evolved in response to the interaction of phenotypic constraints, essential properties of signals, and varied ecological conditions among other factors (Hödl and Amézquita, 2001), underpinned by the need for distinct messages to be transmitted. Sensory channels, whether visual, auditory, or chemical, allow communication of information from one individual that might alter the behavior of another. The signals produced are varied and can act across different spatial scales; examples include the familiar calls of frogs, water-borne pheromones produced by larvae, and the dramatic coloration of some frogs, as well as other visual displays. The information contained in these signals is equally diverse and may relate to warnings and alarms, deterring competition, and mate attraction.

One of the fundamental issues in sexual selection is the sexual dimorphism found in many species where males are more conspicuously ornate than females; males possessing elaborate traits gain improved mating success

when competing for access to females that, in turn, are choosing such traits. Sexual selection theory predicts that individuals may gain more matings through increased attractiveness to individuals of the opposite sex and that certain phenotypic attributes may also be correlated with general physical condition or social hierarchy. Information that enables the assessment of an individual's traits is important for females in particular because, in the majority of species, they invest more time and energy in producing offspring than males. The high investment may make access to reproductive females a limiting factor for males. In male–male interactions, signals can act as a substitute for physical confrontation (avoiding the associated risk of injury). Male signals usually offer information about the individual's condition that underpins the beneficial traits that might be passed on to the next generation, and females recognize these signals and use them in mate choice (Zahavi, 1975). Heritable phenotypic traits may even lead to Fisherian runaway selection where the traits selected by females may no longer be associated with other adaptive male

⁵ CORRESPONDENCE: e-mail, cvn22@cam.ac.uk

characters and are simply beneficial because females still prefer them (Fisher, 1930). Additionally, it has been shown that signal traits might evolve to match already pre-existing preferences for certain signal characteristics based on the capacity of the females' sensory system (Ryan, 1998). Sexual selection plays an important role in signaling and communication and in a recent study female choice in an anuran was found to be based on more than one mode of communication (Rosenthal et al., 2004).

Amphibians are either explosive breeders or have a prolonged breeding period; these form two distinct mating systems at the opposite ends of a continuum (Wells, 1977). In explosive breeders, the reproductive activity of a population occurs during a very short time; females coming to a breeding site have little mate choice, because males start amplexus as soon as they encounter a female. In more prolonged breeders, such as *Nectophrynoides tornieri*, mating takes place over a period of several weeks or months. Only a few females arrive at the breeding site at once, which makes the active search for females (by males) presumably costly and males are selected by their calling activity (Davies and Halliday, 1977; Gerhardt and Huber, 2002; Ryan, 1985; Schwartz, 1986). An attractive male can gain several females in succession, whilst female choice may leave other males without any reproductive success. It is also common for males of prolonged breeding species to establish a small territory during the mating season, which they defend against intruding males; a female frog can compare several males and assess their quality and their territories, and choose the most attractive mate (Pröhl and Hödl, 1999; Roithmair, 1994).

Most anurans depend on acoustic communication (Dorcas et al., 2010) although visual communication is not uncommon (see, for example, Amézquita and Hödl, 2004; Haddad and Giaretta, 1999; Hirschmann and Hödl, 2006; Rosenthal et al., 2004; and review by Hödl and Amézquita, 2001). Although bimodal communication has also been noted through a combination of visual and acoustic signaling (Grafe and Wanger, 2007; Hödl and Amézquita, 2001; Narins et al., 2003), we

report a locomotory reaction to an acoustic signal that may serve as an initial visual display toward conspecific males and that is commonly followed by an acoustic response.

The anuran genus *Nectophrynoides* (Bufonidae) is restricted in distribution to the submontane and montane forests of the Eastern Arc Mountains and the Southern Highlands of Tanzania (Menegon et al., 2007). Tornier's Forest Toad, *Nectophrynoides tornieri* (Roux, 1906), is a viviparous anuran that is endemic to the African Eastern Arc Mountains (Channing and Howell, 2006), being common in the East Usambara Mountains. Barbour and Loveridge (1928) report a clear sexual dimorphism in *N. tornieri*, stating that the sides and ventral surface of the male are uniformly white or grey, whereas the female's underside is translucent.

In amphibians, parental care is associated with terrestrial breeding (e.g., urodeles, Salthe, 1969; anurans, Wells, 1981) and may prevent dehydration or mold growth and/or deters predators (Wells, 1981). This suggests that, although female *N. tornieri* have a high parental investment, they could potentially breed over extended time periods in areas experiencing less favorable conditions than those required by the majority of aquatic breeders. In order to successfully reproduce, females have to find their mate during a breeding season of several months and are attracted to advertisement calls from males; males climb trees and bushes and call from about 30-cm height during the breeding period (Channing and Howell, 2006). The vocalization is a characteristic 'pink' (Channing and Howell, 2006) given as a sequence of single-, double-, or occasionally three- and four-note calls (V. C. Fosah, P. Kamminga, and I. Stamberger, personal observations).

During observations made at the Amani Nature Reserve in the Usambara Mountains, Tanzania, prior to the current study, a considerable number of calling male *N. tornieri* were observed in a peculiar posture. Vocalizing males were observed with their bodies raised above the leaf surface on which they were sitting; they adopted a posture with their fore and hind legs completely extended. Sometimes males remained in the upright posture for some time after they stopped

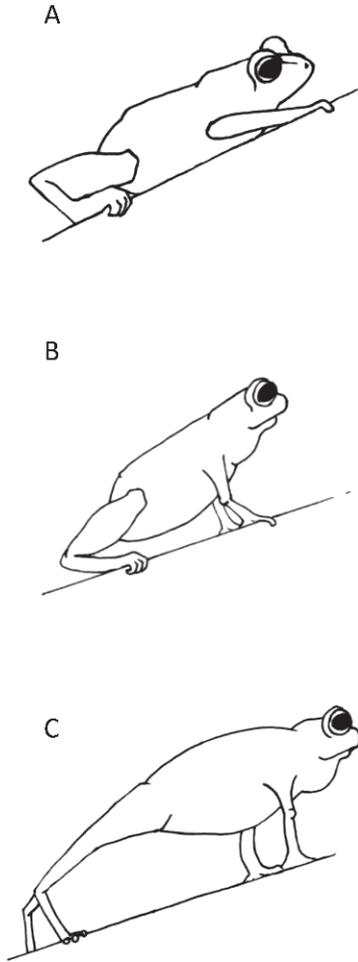


FIG. 1.—Postural change in *Nectophrynoides tornieri* (drawn from photographs taken by J. van Leeuwen, P. Kamminga, and I. Starnberger). (A) Flat position with body and legs pressed to plant surface. (B) Sit-up with fore legs stretched to raise anterior part of body. (C) Push-up with both fore and hind legs fully extended and entire body raised from plant surface.

vocalizing. We, henceforth, describe this posture as the ‘push-up’ (Fig. 1C and see Fig. 1A–B for full postural behaviors).

Following these initial observations, we tested whether the push-up was used by male *N. tornieri* as: a defensive posture to confuse predators by mimicking a larger body size, a visual signal to attract females, or a visual display to deter intruding males. We performed manipulative behavioral experiments using males or females introduced to calling male *N. tornieri*, as well as playbacks of male

calls, to examine the focal male’s response, and determine possible functions of the push-up. Due to the scarcity of information on habitat characteristics favored by *N. tornieri*, we also describe features associated with the microhabitat surrounding male calling positions.

MATERIALS AND METHODS

Study Site

The data were collected in the forest of the Amani Nature Reserve (geographic coordinates of ANR head office: 5.101097°S, 38.629239°E; datum = WGS84) in the East Usambara Mountains, Tanzania, in August 2009. The East Usambaras cover approximately 30,000 ha and comprise 30% submontane forest and 63% lowland forest, much fragmented through human activity. Altitude is the factor differentiating these forest types (Hamilton, 1989), with submontane forest generally occurring above 850 m in elevation; the study site was at approximately 900 m in elevation and most male *N. tornieri* used in the study were found along main trails in the Mbomole Hill area.

Experimental Design

Exploratory field observations revealed that the male calling activity was at its maximum on humid nights, between 2000 h and 0130 h. Individual males were located along paths by their conspicuous push-up postures, or by their calls; such males were repeatedly observed within 1 m² of first sighting, and in most cases were relocated on the same plant or even on the exact leaf used as a calling perch on consecutive nights. Searches during the day did not successfully locate any males; individuals were not marked between initial and subsequent sightings; thus, territoriality, though probable, cannot be assumed. On finding a vocalizing male, manipulative behavioral experiments were carried out under natural conditions using the following procedure.

A tripod with a platform (23 cm × 35 cm) was placed 50 cm from the resident male in all treatments, set to the same height (and never more than 20 cm below the calling male where this was not possible due to steep slope or reaching the maximum extension of the

tripod legs). Forty-nine male *N. tornieri* were exposed to one of the following treatments (the order was randomized for each block of four treatments): control (empty platform positioned close to the calling male; $n = 14$); introduction of a female ($n = 9$); introduction of another male ($n = 13$); playback of a conspecific male call ($n = 13$). The introduced frogs remained on the platform unrestrained for the duration of the introductions.

A male (snout-vent length; SVL = 23.1 cm) and a female (SVL = 24.7 cm) *N. tornieri* from the tested population were caught prior to the study, kept in an enclosure, and these individuals were used for testing responses of all males in treatments 2 and 3. Both individuals were released at the site of capture after the completion of the experiments. Individuals of similar size were chosen to ensure that any reaction in the focal males was likely elicited through gender and not size differences (see Barbour and Loveridge, 1928). The male individual used for introductions was also recorded prior to capture at its natural calling perch using a combined digital audio player and recorder (Sony MZRH1B.EU8 Hi-MD with integrated speakers used throughout; response bandwidth 20–20,000 Hz) and its vocalizations (comprising two-note calls) used for all trials in treatment 4. Using the same equipment, calling males ($n = 9$) were recorded in July 2010 for further characterization of vocalizations. To the human listener, there was no perceptible difference between the playback and the real call (sound pressure level was not recorded) and observations indicated no difference in a male's reaction to either. Sound pressure levels were not recorded but the amplitude of the playback was controlled by maintaining a similar distance between sound source and focal individual, using a fixed volume setting, and by always utilizing fully charged batteries for the audio player.

To achieve identical conditions at the start of each trial, the plant on which the tested male was resident was slightly shaken to trigger a 'flat' posture (see Fig. 1A and Results and Discussion). The treatment was introduced immediately, and behavior was observed for 10 min. The response of the male *N. tornieri* was recorded for the following

behavioral displays: flat position; sit-up position; push-up position (the measured variable was time in seconds in each position). The call pattern was also recorded and timed for the same period. In case of external interferences (e.g., another *N. tornieri* calling nearby or an acoustic interference from another animal), the time and reaction was noted.

After each experiment, the host plant was marked with numbered flagging tape in order to gather data about the microhabitat characteristics the next day during daylight hours. The temperature during all trials ranged from 16°C to 19°C.

Habitat Features

To evaluate the characteristics of the microhabitat utilized for calling position by male *N. tornieri*, a 1-m² plot around the previously marked plant was examined. The following characteristics were recorded: host plant species; the height of the male above ground level; the leaf litter depth; the percentage canopy cover; the estimated percentage cover of vegetation at various heights within the plot (0–0.5 m, 0.5–2 m, 2–5 m), bare ground, rock, and extent of plot on trail; presence of conspecifics within the plot; aspect and slope of the plot.

Data Analysis

The data were analyzed with Minitab statistical software (2000; Release 13.32). Where data were normally distributed, one-way ANOVAs were used to test dependent variables (time in seconds for each behavior within observation period) versus treatment (independent variable). Nonparametric tests (Mann-Whitney *U*) were used to test differences in the median time to first vocalization where data were not normally distributed. Results are reported ± 1 SE of the mean. We analyzed the calls using Raven Pro 1.3 (build 32) software for Windows.

RESULTS

Call Characteristics

The call of *N. tornieri* is a distinctive, slightly metallic 'pink,' in almost all instances commencing with a single note before progressing to a rapid, repetitive, double note. In rare cases, outside our manipulative experi-

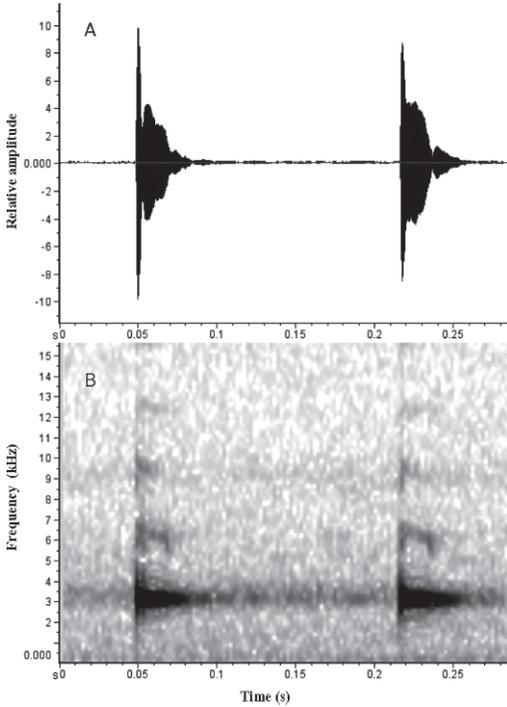


FIG. 2.—Double-note advertisement call of *Nectophrynoides tornieri*: (A) spectrogram and (B) corresponding waveform.

ments, we heard males producing triple notes followed very occasionally by quadruple notes. The calls could be easily perceived from distances up to 25 m. Males of *N. tornieri* ($n = 9$) produced calls of mean duration 0.19 ± 0.02 s consisting of 1–4 notes (mean note duration 0.04 ± 0.01 s) separated by silent internote intervals (mean duration 0.31 ± 0.50 s). There was no apparent gross temporal pattern in call production amongst individuals (mean intercall interval 1.43 ± 0.06 s). The peak energy of the notes was between 3033.5 and 3205.8 ± 22.2 Hz with additional harmonic frequency bands at approximately 6100, 9400, and 12,400 Hz. A sonogram of a typical advertisement call of *N. tornieri* in the studied population is shown in Fig. 2 and a short video sequence showing the calling behavior of the male will be made available on www.amphibiaweb.org.

Locomotory Responses

The initial reaction to disturbance in all individuals ($n = 49$) was to flatten themselves

to the substrate; this flat position was maintained throughout the experimental period by 23 individuals. The remaining focal individuals (all of which stayed on their original calling perch) produced movements, usually in a set sequence; introduced males and females also remained on the platform, most often in a static position and rarely hopping. Introduced males occasionally adopted a sit-up position; the push-up posture was only observed in the resident focal males.

During the control experiments ($n = 14$), the majority of the tested males remained in the flat posture; four individuals produced a sit-up and, of these, two progressed to a push-up. Of the four males in sit-up, one returned to the flat posture and of the two males in push-up, one returned to a flat posture.

Introducing a female ($n = 9$) did not affect time spent in either sit-up or push-up positions. Six resident males did not react when females were introduced and remained in the flat posture for the whole time period. Only two males displayed a sit-up and one of these continued to the push-up position with the other returning to a flat posture. The remaining male went from a flat posture to a push-up display without performing a sit-up display and was the sole individual in all treatment groups to produce this behavior.

When a male was introduced, sit-up display increased over time, thereby reducing time spent in the flat position. Nine of the 13 males (69%) in this treatment group exhibited a sit-up display but no subsequent push-up followed. One male returned from a sit-up position to the flat posture.

The playback treatment produced the greatest locomotory response; 9 of 13 males performed sit-up and push-up displays with the majority of individuals progressing through the full behavioral repertoire (Fig. 3). During the experiment, four focal males returned from a push-up to a sit-up and two of these then adopted a flat posture.

Male *N. tornieri* spent significantly less time in the flat position when subjected to conspecific calls in comparison to other experimental treatments (one-way ANOVA; $F_{3,45} = 3.63$, $df = 3$, $P = 0.02$); post hoc tests (Tukey's multiple pair-wise comparison) found differences between playback and both

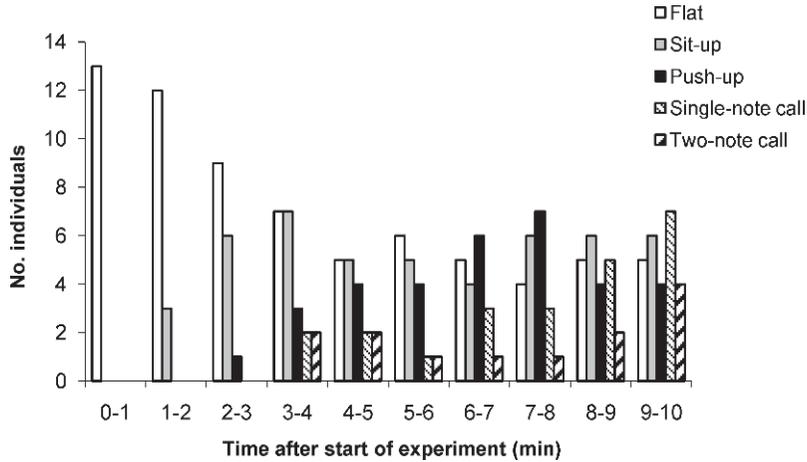


FIG. 3.—Change in behavior by male *Nectophrynoides tornieri* during 10-min period following introduction of playback call by conspecific male.

female introduction and control treatments but not between playback and male introduction treatments (Fig. 4). Mean time to the production of the first sit-up display was 301.3 ± 67.1 s when a male was introduced and 200.0 ± 47.2 s in the playback group. This difference was not statistically significant (Mann–Whitney test, using medians: $W = 100.5$, $P = 0.4140$) and no meaningful statistical comparisons could be made with the control and female introduction groups due to very low response levels. The mean time to first push-up was 299.9 ± 44.1 s in the

playback group, the only treatment where a mean time could be established. Hence, the locomotory response to playback calls was greater than in any of the remaining treatment groups.

Vocal Responses

Eighteen of 49 tested males produced vocalizations following adoption of the sit-up or, most often, the push-up. Of these, all but one exhibited the typical vocalization sequence of a short period of single notes, followed by a bout of two-note calls. One

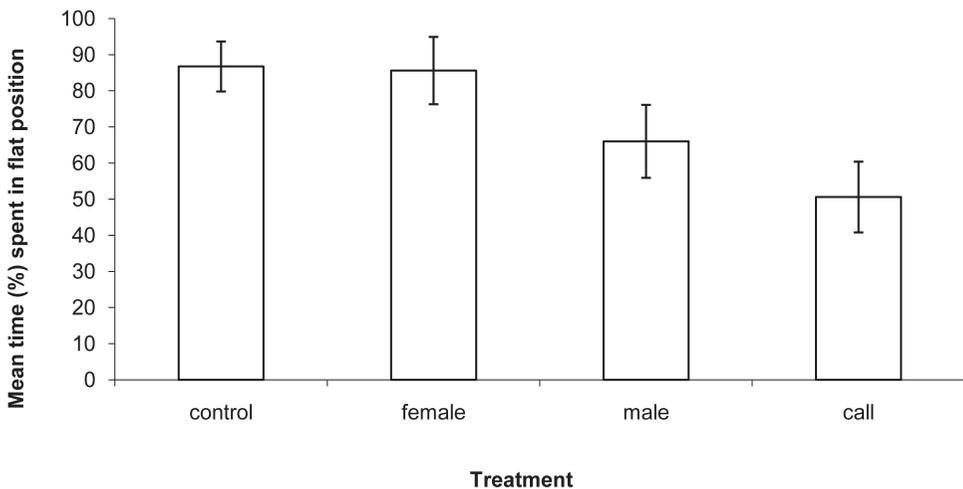


FIG. 4.—Proportion of time (%) in full observation period spent in flat position by male *Nectophrynoides tornieri* following introduction of experimental treatment.

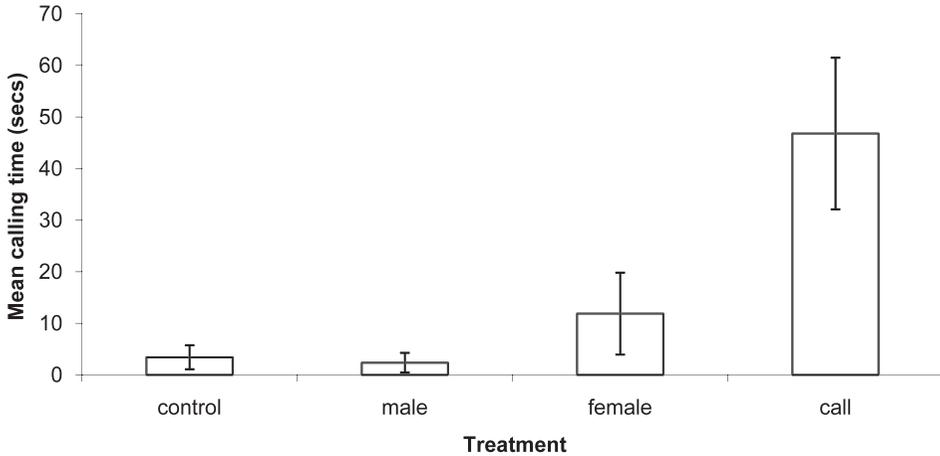


FIG. 5.—Mean time (s) within 10-min period spent calling by male *Nectophrynoides tornieri* in 10-min period following introduction of experimental treatment.

individual began with a two-note call and almost immediately followed with single-note calls. Three introduced males gave single-note calls in response to calls from the focal male. Just two males in each of the control ($n = 14$) and female introduction ($n = 9$) groups produced calls, whereas the introduction of a male ($n = 13$) lead to vocalizations in four tested males and playback calls initiated calling in ten males ($n = 13$). In the playback group the mean time to production of the first single-note call was 383.7 ± 49.9 s; for the seven males that progressed to two-note calls the mean time to switch call type was just 19.57 ± 3.3 s. Overall, tested males spent significantly more time calling within the experimental period in response to playback calls than when either males or females were introduced, or under control conditions (one-way ANOVA: $F = 6.45$, $df = 3$, $P = 0.001$); post hoc tests (Tukey's multiple pair-wise comparison) confirmed differences between playback and all other treatments (Fig. 5). Hence, vocalization in *N. tornieri* was strongly linked to conspecific calls.

Microhabitat Characteristics

Male *N. tornieri* were found on 27 different host plants (Table 1), most often on *Clidemia hirta* (16%) and *Marattia fraxinea* (10%), and at a mean height of 79.83 ± 4.69 cm from the ground (median = 70.0 cm, range = 40–170 cm). An earthen trailside bank was

present in nearly three-quarters of the territories and none of the males were found in or near forest gaps along the trail (daytime observation). There were no other apparent common features found between calling position and microhabitat characteristics.

DISCUSSION

Of three competing hypotheses to explain the function of the push-up posture in calling male *N. tornieri*, this study indicates that the behavior is most likely a visual display to deter intruding males with the possibility that improved transmission of the call also plays a role (either to attract females or further repel other males). Also, we report in detail for the first time the characteristics of vocalizations in this species.

Of the three initial alternatives for the utility of the push-up, a defensive posture seems least likely; the initial reaction by all males to disturbance by the experimenters was to adopt the flat position. This suggests that the frogs are reacting to possible danger by flattening themselves against the plant surface (Fig. 1A) to make themselves less visible, rather than creating a larger image that would be the case with the push-up when raised from the substrate (Fig. 1C). Although jumping is the main escape and survival ploy for most adult frogs, other strategies have been noted. Deimatic behavior, such as display of warning markings and changes of

TABLE 1.—Plant species utilized as calling sites by male *Nectophrynoides tornieri* ($n = 49$).

Species	Family	Proportion of frogs observed calling on each plant species
<i>Clidemia hirta</i>	Melastomataceae	16%
<i>Marattia fraxinea</i>	Marattiaceae	10%
<i>Blotiella</i> sp.	Demnstaedtiaceae	6%
<i>Bolbitis gemmifera</i>	Lomariopsidaceae	6%
Sp. 3	Rubiaceae	6%
<i>Cephalosphaera usambarensis</i>	Myristicaceae	4%
<i>Cinnamomum camphora</i>	Myristicaceae	4%
<i>Cyathea manniana</i>	Cyatheaceae	4%
<i>Dracaena deremensis</i>	Dracaenaceae	4%
<i>Hypolytrum testui</i>	Cyperaceae	4%
<i>Syzygium</i> sp.	Myrtaceae	4%
<i>Aframomum</i> sp.	Zingiberaceae	2%
<i>Alchornea hirtella</i>	Euphorbiaceae	2%
<i>Annickia kummeriae</i>	Annonaceae	2%
<i>Asplenium nidus</i>	Aspleniaceae	2%
<i>Costus sarmentosus</i>	Zingiberaceae	2%
<i>Cyclosorus</i> sp.	Thelypteridaceae	2%
<i>Dracaena laxissima</i>	Dracaenaceae	2%
<i>Justicia anagalloides</i>	Acanthaceae	2%
<i>Memecylon cogniauxii</i>	Melastomataceae	2%
<i>Memecylon</i> sp.	Melastomataceae	2%
<i>Maesopsis eminii</i> (dead twig)	Rhamnaceae	2%
<i>Sorindeia madagascariensis</i>	Anacardiaceae	2%
<i>Whitfieldia elongata</i>	Acanthaceae	2%
Sp. 1	Annonaceae	2%
Sp. 2	Euphorbiaceae	2%
Sp. 4	Rubiaceae	2%

body shape, has been reported in frogs (e.g., Das et al., 2010; Lenzi-Mattos et al., 2005; Martins, 1989); these responses entail threatening postures and reactions found in diverse taxa, including insects, reptiles, and mammals, when dealing with potential predators. In *N. tornieri*, the opposite occurs as individuals reduce their appearance when disturbed and the push-up position is most often elicited under other circumstances. Complete lowering of the body has been noted before (Hödl and Amézquita, 2001) and submissive behavior is the most likely explanation.

Throughout the study, all male frogs displayed the behavioral responses in a particular sequence and the push-up posture was strongly associated with call production (Fig. 3). Males exposed to the playback of another male's call spent less time in flat position (Fig. 4), but more in both sit-up and push-up postures. Moreover, these males were more likely to initiate calling and spent more time calling than in other treatments (Fig. 5). The reaction to an introduced male was similar but less pronounced unless the

introduced male started to vocalize; this leads us to assert that the acoustic cue is a very important stimulus for *N. tornieri*. Furthermore, our results show that male *N. tornieri* never call in the flat position and rarely call in sit-up position. This suggests that calling is linked with the push-up position and that both signals are produced in response to other males, possibly combining as an aggressive display. The stronger reaction in movement and calling response to playback than to female *N. tornieri* suggests that the behavior is directed toward conspecific males.

We did not unequivocally determine whether the behavior is aimed at attracting females or defending calling perches from rival males; the locomotory movements reported in this study represent a novel sequence of movements that may serve either purpose. Adoption of the push-up posture for calling could be beneficial for the male frog as both an aid to sound transmission and—or as a close-range visual cue. Equivalent positions to the push-up have been previously recorded; 'lifting of the body' during territorial disputes

in the diurnal frog *Hylodes asper* has been described by Haddad and Giaretta (1999) and 'body raising' is documented by Hödl and Amézquita (2001), although neither study relates the behavior to calling. Many anurans stretch their fore legs to adopt an upright posture (or sit-up) in various contexts but these have not been considered as a visual display (Hödl and Amézquita, 2001). Here, the full push-up position may act as a visual display because the ventral surface of the males always appeared brighter than the dorsal skin to the human eye (V. C. Fosah, P. Kamminga, and I. Starnberger, personal observations; and see Barbour and Loveridge, 1928). The change of posture itself is likely to alter visual appearance and allow visiting females or males to more easily locate resident calling males, with the posture potentially exposing the lighter parts to further enhance the image (and see Sztatecsny et al., 2010). In this study, the visual display always precedes vocalization and may allow approaching conspecifics to rapidly distinguish whether the resident is a potential mate or competitor. Grafe and Wanger (2007), Böckle et al. (2009) and Preininger et al. (2009) all reported calls that acted as an alert signal and are usually followed by a visual signal (e.g., foot-flagging); in *N. tornieri* the acoustic signal was always produced after the change of posture. Rosenthal et al. (2004) found that female *Engystomops pustulosus* preferred males where the added stimulus of an inflated vocal sac was visible to those without; a combination of visual and vocal cues used by female *Hyla arborea* in choice of mate was found to vary between individuals in manipulative experiments by Richardson et al. (2010). Visual display in a nocturnal frog is uncommon, though relatively understudied (but see Gomez et al., 2009; Taylor et al., 2007; Vasquez and Pfennig, 2007) and the phenomenon in diurnal frogs is most common in habitats where ambient noise levels are high (e.g., by fast-running streams and waterfalls). Because this is not the case for the terrestrial *N. tornieri* at Amani (and although the possibility of bimodal communication cannot be ruled out), the push-up posture is possibly associated with an aspect of sound transmission.

Amplitude and frequency of the call may be a cue used by females for mate selection (Ryan, 1980) and it is possible that vocalizing in the push-up posture might improve call quality and/or transmission for *N. tornieri* through inflation of the lungs or the vocal sac to their full extent. Pombal et al. (1994) described a 'high posture' in calling male *Brachycephalus ephippium* and linked this to the enlarged vocal sac that reached down to the chest. No morphometric measurements of the vocal sac were made for *N. tornieri* and further investigation of call volume, the modulation of calls, frequency, and their correlation to body size would be helpful to better understand the behavior of the resident males. Further manipulative experiments could also enlighten female choice criteria.

We found no obvious microhabitat features common to calling positions; however, in contrast to Channing and Howell (2006), who suggested a calling height of 30 cm, we found a mean calling position nearly three times higher than this. Greer and Wells (1980) presented evidence that call heights >60 cm lead to increased mating success for male *Hyalinobatrachium fleischmanni*, but noted that aspects of the male display or attributes of the territory may also be important. Other studies have also highlighted the effects of position of calling frogs in relation to sound propagation, transmission, and attenuation (e.g., Kime et al., 2000; Parris, 2002; Penna and Solis, 1998) and the acoustic properties of the calling microsite can also be crucial (Wells and Schwartz, 1982). Whether these factors, in combination with the unusual calling posture of male *N. tornieri*, are important in enabling females to more easily locate potential mates remains to be studied.

Although visual signaling to attract females is a possibility, our findings support the hypothesis that the push-up posture of *N. tornieri* is a calling posture, which serves as a close-range visual threat to intruding males or may modulate some aspect of the call that deters such conspecifics. More research is necessary to assess the relative importance of the cues and establish whether bimodal signaling is taking place. Certainly, while the presence of another male mostly evokes sit-up displays, the male call seems to be necessary

to evoke a display of the push-up position and reciprocal calling. Additionally, a lesser reaction to female presence indicates that the push-up is a component of a male–male agonistic interaction as opposed to a mate attraction display.

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