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Vocal Repertoire and Calling Activity of a Dwarf Clawed Frog (*Hymenochirus boettgeri*)

Most anurans (frogs and toads) are highly vocal, and rely on acoustic communication to mediate social interactions and mate choice (Ryan 2001; Gerhardt and Huber 2002; Wells 2007). Many species have vocal repertoires consisting of several different types of calls produced in different behavioral contexts (reviewed in Wells 2007). The most commonly uttered vocalization is the advertisement call, whose primary function is to attract conspecific females from a distance. In some species, males and females produce close-range courtship calls that can further influence mating decisions. Many species also have release calls; these are vocalizations given by either other males

or unreceptive females when clasped by a male, and function to facilitate release from unwanted amplexus (Tobias et al. 2014). Vocalizations are also involved in mediating male-male interactions. The advertisement call, and frequently also special aggressive or encounter calls, may function in determining inter-male distances within the chorus or settle disputes over calling sites and territories (reviewed in Wells 2007). Thus, vocalizations play important roles in sexual selection by both female choice and male-male competition. Despite the obvious importance of vocalizations for the behavioral ecology of frogs and toads, detailed descriptions of the vocal repertoire and patterns of calling activity are available for only a relatively small subset of species (Bee et al. 2013). Yet, such descriptions can give a better idea about the richness of social interaction found in anurans, and guide further research on topics ranging from mate choice to call evolution and systematics to community ecology.

There is considerable diversity of calls and larynx morphologies among frogs, but the vast majority of species produce airborne vocalizations; here, a call is produced by moving air from the

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lungs through the glottis and call production is associated with the conspicuous inflation of the male's vocal sac (Duellman and Trueb 1994). A notable exception from this general pattern occurs in frogs of the family Pipidae, which includes the South American Surinam toads (genus *Pipa*) and the African clawed frogs (genera *Hymenochirus*, *Silurana*, *Xenopus*, and *Pseudhymenochirus*). Pipids are fully aquatic frogs, with unique biology, morphology, and call production mechanism (Cannatella and Trueb 1988; Yager 1992). As a consequence of their unique call production mechanism, which relies on bony rods in the larynx to produce clicking sounds (Yager 1992), vocalization occurs largely without externally visible movements of the flanks or throat (Rabb 1960; Österdahl and Olsson 1963; Rabb and Rabb 1963; Weygoldt 1976; but see Irisarri et al. 2011). This motionless calling is performed underwater making it next to impossible to ascertain which individual is producing the vocalization, thus hindering observations of behavioral interactions. Despite these difficulties, advertisement calls have been described for 22 species of *Silurana* and *Xenopus* frogs (Tobias et al. 2011), and the data suggests a rich and varied vocal repertoire. The temporal structure of their

calls varies from simple single clicks to complex calls with two temporal patterns, and some species have vocal repertoires consisting of multiple call types (Tobias et al. 1998; Tobias et al. 2011; Tobias et al. 2014). For example, in *Xenopus laevis*, the most well-studied species of the clade, females produce two types of calls (ticking and rapping calls), and males produce six types of calls (advertisement call, amplexant call, answer call, chirps, ticks and growls). Chirps are given during male-male interactions, and growling accompanies male-male clasping and may function as a release call (Tobias et al. 2004; Tobias et al. 2014).

The objective of this study was to provide a quantitative description of the vocal repertoire of the Dwarf Clawed Frog *Hymenochirus boettgeri*, and to ascertain the social contexts in which each vocalization is produced. Previous studies on the reproductive behavior of this species have focused on their use of chemical communication (Pearl et al. 2000), yet males do call and the function of these calls is largely unknown (but see Österdahl and Olsson 1963; Rabb and Rabb 1963). We staged different social contexts (solitary, single sex groups, mixed sex groups), and collected automated recordings using a hydrophone to sample patterns of calling activity and types of vocalizations to decipher the communicative significance of acoustic signals in the social behavior of this species.

METHODS

Study animals and recording setup.—We conducted the study between 14 February and 6 April 2011 with *H. boettgeri* frogs (Fig. 1; N = 5 females and 15 males) obtained from a local pet store (Hoffer's Tropical Life Pets, Milwaukee, Wisconsin, USA). All 20 frogs were obtained at the same time, making it likely that they came from the same supplier and were related. We housed animals in same sex groups in four 57-L aquariums with gravel, live plants, and PVC pipes as hiding places. Each of these maintenance tanks contained a small filter and a heater



FIG. 1. Male *Hymenochirus boettgeri*.

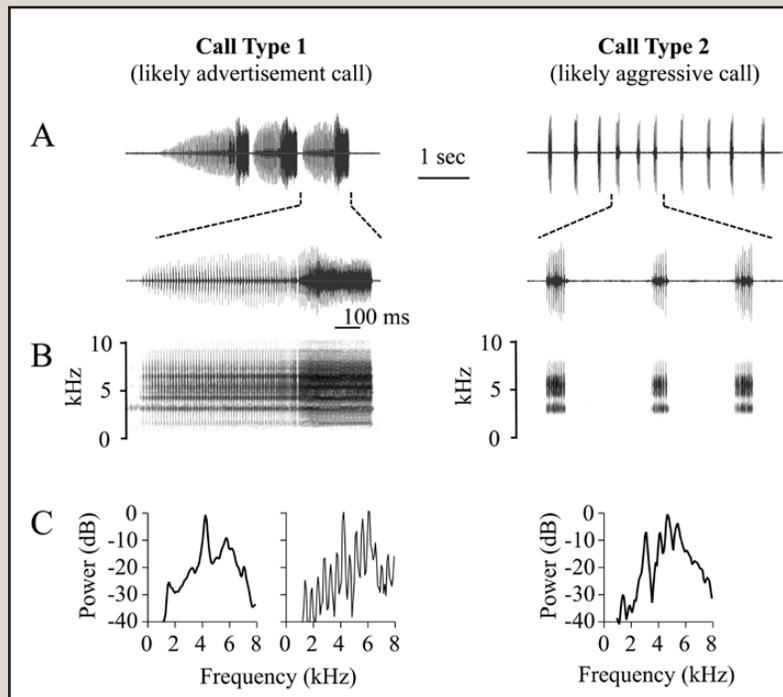


FIG. 2. Calls of *Hymenochirus boettgeri*. A) Waveforms of a call sequence of Type 1 calls (left, top trace: three calls of one male; bottom trace: zoomed in view of one call) and of Type 2 calls (right, top trace: 11 calls of one male; bottom trace: zoomed in view of three calls). B) Spectrograms of a Type 1 call (left) and three Type 2 calls (right). C). Powerspectra of the two elements of a Type 1 call (left), and of a Type 2 call (right).

that maintained the water temperature at 25°C. Tanks were illuminated by strip lights with a 12 h/12 h light/dark cycle, set to switch on at 0800 and off at 2000 hrs.

We recorded frog calls with a Song Meter MS2 hydrophone connected to a Song Meter SM2+ automated recorder (Wildlife Acoustics, Inc., Massachusetts, USA). The recorder was programmed to record for 10 minutes every hour at the hour. The recording tank was housed in the same room as the maintenance tanks. The maintenance tanks and the recording tank were similar in setup, except that the filter was switched off during recording sessions to improve recording quality.

Experimental design.—We examined the importance of sex and social context on calling activity and call type production by comparing recordings that were obtained when the recording tank contained (i) only one female (N = 3; each recorded for 24 h); (ii) only one male (N = 3; each recorded for 24 h); (iii) a group of two males (N = 3 groups, comprised of different combinations of individuals; each group recorded for 24 h); or (iv) a mixed sex group of two males and one female (N = 4 groups; different combinations of individuals; recorded for 1 d, 2 d, 5 d, and 11 d, respectively). In general, we did not re-use frogs across treatments, except for two females that participated in both the female only and the mixed sex groups, and two males that participated in the two-male treatment and then, after adding a female, were also recorded in the mixed sex treatment. In total we obtained 660 10-min recordings, 43% of which contained at least one vocalization.

We first conducted a qualitative analysis of the vocal repertoire by grouping vocalizations into categories based on auditory and visual (spectrograms) comparison (Fig. 2). To obtain a quantitative description of the calls in the vocal repertoire, we subsequently selected 10 calls of each call type from 10 different males for detailed analysis (i.e., we analyzed a total of 100 Type 1 and 100 Type 2 calls). We selected calls for detailed analysis based on optimal signal-to-noise ratio. Although we did not mark frogs for individual identification, the sequential nature of the recording sessions, and the fact that we did not re-use males in subsequent trials, allowed us to assign recordings to different males. For recordings from treatments that had more than one male calling at the same time in the recording tank, we used relative amplitude to assign calls to different males. Although this did not allow us to assign calls to individual males, it still meant we analyzed calls from different individuals (which is adequate for our purpose of describing a species' call repertoire). We analyzed calls with Raven Pro v.1.3 (Cornell Lab of Ornithology), and measured the following call properties: (i) number of calls per bout (calls were generally given in bouts of several calls), (ii) call duration (time from onset of call to offset of call), (iii) call period (time from onset of call to onset of following call), (iv) pulse period (time from onset of pulse to onset of following pulse; Nota Bene: this call trait is referred to as "pulse" in the general frog call literature, but often called a "click" in descriptions of pipid frog calls), and (v) dominant frequency (measured separately for each call element in the Type 1 calls; see below). General descriptions of the call types and their variability are based on the raw data (N = 100 calls / type). We then calculated averages for the calls of each male (N = 10), and used those average values to compare traits between call types. Because we would not have been able to attribute a call on our automated recordings to a specific caller's identity (except in the three single male trials), we did not measure male size, and can therefore not test whether certain call properties are correlated with body size.

We further analyzed the pattern of calling activity. For this we scored each of the 660 recordings for the presence or absence of calls (scored as 1 or 0, respectively); if vocalizations were detected, we further scored them for the call type that was given. We only scored presence/absence of call type, not number of calls per recording.

Statistical analysis.—We compared the different elements of the Type 1 call, as well as the two call types overall. Type 1 calls are complex calls. To test whether the two elements comprising a Type 1 call are different, we used a mixed model (Standard Least Squares; EMS), with an α of 0.05. We entered different call parameters as response variables, and call element and male ID as fixed factors (we entered male ID to account for the fact that each male contributed data for both the first and second call element). Although some comparisons showed unequal variances, we did not correct for that because mixed models are robust to violations of statistical assumptions.

When comparing different call types, we visually inspected histograms to verify normal distribution, and used Levene's test to check for equal variances. We then compared data showing equal variances using ANOVA, and those showing unequal variances using Welch ANOVA. We compared overall call duration, pulse period and dominant frequency between Type 1 and Type 2 calls, using an α of 0.05. Because Type 1 calls are complex calls whose two call elements differ in pulse period, we ran this comparison with the Type 2 call twice, once comparing the first, and once the second element of the call. For this comparison we adjusted the α to 0.025. All statistical analyses were computed in JMP Version 8.0 (SAS Institute, Inc., Cary, North Carolina, USA).

RESULTS

Call repertoire.—Solitary males, and males in groups (e.g., two-male and mixed sex treatments) called spontaneously, and we identified two call types (Table 1, Fig. 2) with putatively discrete communicative significance. Recordings from solitary females never registered any vocalizations. Recordings of mixed sex groups did not contain additional vocalizations that had not also occurred in recordings from the two-male treatment, suggesting that females also did not vocalize in social settings.

A representative Type 1 call is shown in Fig. 2 (left) (see also Table 1). Type 1 calls can occur singly, but are generally given in a few calls per bout. These calls are characterized by having a complex call structure (two elements). The first element has a longer call duration and pulse period than the second element (Fig. 3A, B). The dominant frequency of the two call elements is not significantly different (Fig. 3C), but the second element can have a slight upward frequency sweep, and generally shows visible harmonics (see Fig. 2C). Acoustically this call resembles the sound made by repeatedly twisting the cork of a wine bottle.

A representative Type 2 call is shown in Fig. 2 (right). Type 2 calls are given in more calls per bout, and are characterized by having a simple call structure (one element). Acoustically these calls resemble a repeated "kreek" sound. Type 2 calls have a higher number of calls per bout, shorter call duration, and shorter call period (Table 1, Fig. 4A, B, C). The dominant frequency does not differ between call types (Fig. 4D), but note the frequency composition (i.e., density of harmonics) is quite different between the calls (see Fig. 2C). The pulse period of Type 2 calls is similar to that in the first call element of Type 1 calls, but longer than the pulse period in the second element of Type 1 calls (Fig. 4E). Overall, Type 1 calls are given more frequently than Type 2

TABLE 1. Parameters of the two call types recorded from *Hymenochirus boettgeri* males; presented are mean \pm SD and the range (in parenthesis).

Call Parameter	Call Type I	Call Type II
# Calls /Bout	5.6 \pm 3.3 (1–14)	29 \pm 21 (14–84)
Call Duration	908 \pm 371 ms (168–2542 ms)	73 \pm 27 ms (22–277 ms)
Call Period	1024 \pm 399 ms (223–2576 ms)	413 \pm 167 ms (110–1186 ms)
# Call Components	2	1
Duration		
1 st Component	605 \pm 357 ms (168–2100 ms)	
2 nd Component	305 \pm 78 ms (168–578 ms)	
Rel. Duration 1 st Component (%)	57 \pm 14 % (35–89)	
Pulse Period		
1 st Component	8.5 \pm 1.4 ms (5.3–12.8 ms)	8.0 \pm 1.1 ms (6.2–13.6 ms)
2 nd Component	3.6 \pm 1.4 ms (1.9–6.7 ms)	
Dom Frequency		
1 st Component	5169 \pm 813 Hz (3989–6288 Hz)	5081 \pm 603 Hz (3101–6424 Hz)
2 nd Component	5091 \pm 745 Hz (4048–6289 Hz)	
Relative Amplitude (Ampl. 2 nd – 1 st Component)	3.1 \pm 6.1 dB (-15.2–13.2 dB)	

calls (Fig. 5). While either call type can be heard in isolation, Type 2 calls are generally associated with Type 1 calls: 91.4 % of times we observed Type 2 calls, they occurred on the same recordings that also contained Type 1 calls ($r = 0.67$, $P = 0.0004$). No call type was specific to the mixed-sex group social context, i.e., whenever two males were together both call types could be heard, and the presence of a female did not result in additional call types. Sometimes males produce intermediate calls that started as Type 1 calls, but ended as Type 2 calls; the reverse (starting as Type 2 and ending as Type 1) was never observed.

Calling activity.—In both solitary males (Fig. 5A) and groups of males (Fig. 5B, C), calling activity peaked during the early nighttime hours. For solitary males, only Type 1 calls were registered (Fig. 5A), while both call types were registered for groups of two males, and mixed-sex groups (Fig. 5B, C). Calling activity of Type 1 calls increased and peaked earlier than Type 2 calls (Fig. 5), and this pattern was particularly prevalent in mixed-sex groups (Fig. 5C). In trials where no female was present, calling activity of Type 1 calls (Fig. 5A,B) showed a narrower peak (3–5 h/night), while high calling activity persisted over a longer period of time when females were present (about 9 h/night, Fig. 5C).

In anurans, vocal repertoires can be complex and comprise several distinct call types (Höbel 2000; Narins et al. 2000; Christensen-Dalsgaard et al. 2002; Feng et al. 2002; Tobias et al. 2004). Nevertheless, most species seem to have only two or three call types in their repertoire (Rand and Ryan 1981; Wells and Greer 1981; Kanamadi et al. 2001; Bee et al. 2013). We found that the vocal repertoire of male *H. boettgeri* contains at least two call types, with probably different communicative significance. However, because we never observed mating / amplexus during our trials, it is possible that we did not capture the entire vocal repertoire of this species. Although we currently do not know the different functions (if any) of the two described call types of *H. boettgeri* with certainty, comparison with other frogs allows us to speculate about their putative functions.

Advertisement calls serve the dual function of attracting females and advertising male position to other males (Gerhardt and Huber 2002; Wells 2007), and, in *Xenopus*, they also serve to suppress calling in conspecific males (Tobias et al. 2010). Four observations suggest that the Type 1 call of *H. boettgeri* is the species' advertisement call. First, Type 1 calls are the most frequently given call type. Second, this call type was registered in all social contexts suggesting that it is geared towards both males and females. Third, in the absence of competition (i.e., solitary males), only Type 1 calls occurred; this rules out an encounter or aggressive function of this call type. Fourth, in trials where a female was present, high calling activity of Type 1 calls persisted over a longer period of time than in trials that did not include a female, suggesting that the presence of females motivated males to call.

Generally, the dual-purpose function of advertisement calls (mate attraction / male position advert) is achieved with a "simple call," i.e., a call consisting of one uniform acoustical element (Gerhardt and Huber 2002; Wells 2007). In some species, however, such as the Puerto Rican Coqui (*Eleutherodactylus coqui*) or the Túngara Frog (*Physalaemus pustulosus*), males produce "complex calls" comprised of two acoustically distinct elements. Here, one element is geared more towards males, and the other more towards females (Narins and Capranica 1976, 1978; Rand and Ryan 1981). The Type 1 calls of *H. boettgeri* consist of two acoustically different call elements, i.e., they are complex calls, and the different call elements may have different intended receivers and serve different communicative purposes. Because the first call element of the Type 1 call is more similar to the Type 2 call, spectrally and in its fine pulse structure, we speculate that the first element is directed towards males, and the second is directed towards females. Playback experiments are needed to verify this hypothesis.

Type 2 calls were not observed in recordings of solitary males, suggesting that it is not another type of advertisement or courtship call. Rather, because Type 2 calls were only observed in situations where two males could interact with each other both vocally and physically, this vocalization could be a release call or an aggressive call. Since we did not conduct visual observations concurrent with the acoustic sampling, we do not know whether the Type 2 call was given only in response to clasping attempts between males, i.e., whether this call type is a release call. Additional experiments, either via visual surveys or by having males in the same tank, but physically separated by chemically and acoustically transparent dividers, would be needed to confidently exclude the possibility that this call type is a release

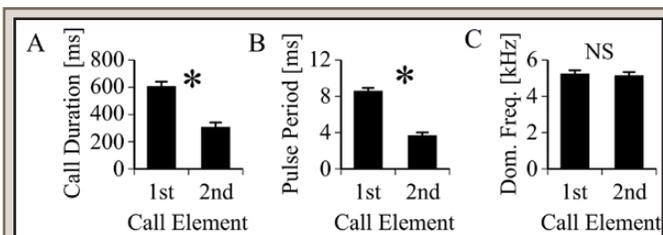


FIG. 3. Differences between the first and second element of Type 1 calls. A) Duration ($F_{1,19} = 28.97$, $P < 0.0001$) and (B) pulse period ($F_{1,19} = 67.77$, $P < 0.0001$) were significantly different between the two elements of the Type 1 call, but (C) dominant frequency was not ($F_{1,19} = 0.09$, $P = 0.77$). Shown are least square mean \pm SE. Significant differences indicated by asterisk. Male ID was never significant (data not shown).

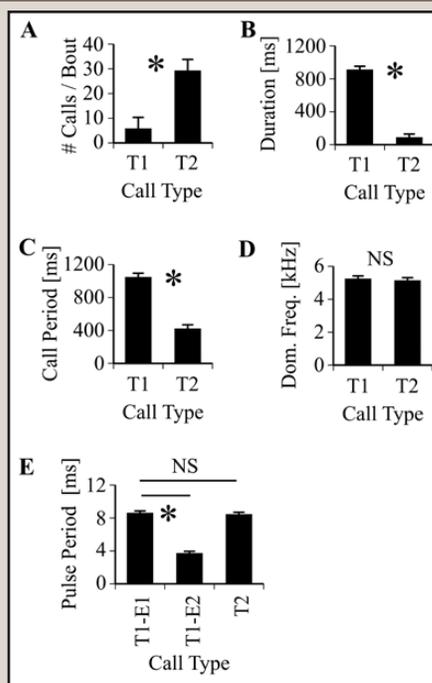


FIG. 4. Differences between the two call types. A) The number of calls per bout (Welch ANOVA: $F_{1,9.44} = 11.82$, $P = 0.007$), (B) call duration (Welch ANOVA: $F_{1,9.47} = 136.5$, $P < 0.0001$), and (C) call period (Welch ANOVA: $F_{1,9.94} = 62.6$, $P < 0.0001$) were significantly different between call types. D) Pulse period of the Type 2 call was not different from the first element of the Type 1 call (ANOVA: $F_{1,19} = 0.12$, $P = 0.74$), but significantly different from the second element of the Type 1 call (Welch ANOVA: $F_{1,13.33} = 111.3$, $P < 0.0001$). E) Dominant frequency also did not differ between call types (ANOVA: $F_{1,19} = 0.13$, $P = 0.73$), but note the difference in frequency composition between the calls (see Fig. 2C). Shown are mean \pm SE. Significant differences indicated by asterisk.

call. However, since only the clasped male should produce a release call, yet we have several recordings where both males were giving this call simultaneously, we think it is more likely that the Type 2 call is the species' aggressive call.

Aggressive calls can be distinct or graded. In graded aggressive calls, an increase in aggressive intent is reflected by the addition of more calls or call notes (Wagner 1989; Wells 1989). For example, male Blanchard's Cricket Frogs, *Acris crepitans blanchardi*, respond to increased sound pressure level of rival male calls (i.e., to increased rival proximity) by producing progressively longer

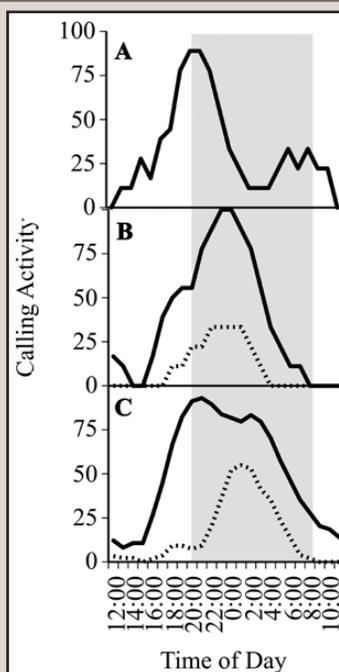


FIG. 5. Calling activity of single males (A), groups of two males (B) and mixed-sex groups (C). Calling activity of Type 1 calls is shown as solid black line, that of Type 2 calls in dashed line. The shaded area indicates periods of darkness (i.e., lights out).

call bouts, longer calls with more pulses, and more pulse bouts per call (Wagner 1989). The call bouts of *H. boettgeri* Type 2 calls can range in size from 14–84 calls/bout, suggesting the presence of a similarly graded aggressive call display.

Although we suggest that Type 2 calls are involved in antagonistic interactions between males, the particular behavioral context is less clear. Since Type 2 calls increase in prevalence only after the activity of Type 1 calls is already increased or peaked, these calls probably do not function in regulating inter-male distances during nightly chorus establishment, as is the case with aggressive calls during chorus formation in many species of frogs (Wells 2007). There, aggressive calls occur more frequently during the initial portion of nightly chorus formation, and diminish in prevalence once calling sites are established and males switch to giving predominantly advertisement calls (Dyson and Passmore 1992). The concurrent nature of both call types in *H. boettgeri* also suggest that Type 2 calls are not involved in call suppression behavior similar to the one described for another pipid frog, *Xenopus laevis*, where after initial chorus formation males induce rivals to fall silent until only the dominant male remains calling (Tobias et al. 2010).

Multimodal communication in anuran amphibians.— In contrast to the large number of studies on chemical communication in caudate amphibians (reviewed in Houck 2009), there are few documented examples of the use of chemical communication in adult anurans (review: Belanger and Corkum 2009). Nevertheless, some adult anurans use chemical cues for sex recognition and mate attraction (Wabnitz et al. 2000; Waldman and Bishop 2004; Asay et al. 2005; Byrne and Keogh 2007), and *Hymenochirus* frogs are among the few species for which chemical mate attraction has been experimentally documented (Pearl et al. 2000). *Hymenochirus* mate attraction chemicals are produced by the postaxillary breeding glands of adult males (Pearl et al. 2000), which develop during sexual maturation and

enlarge during the breeding season (Rabb and Rabb 1963). In a y-maze, female *Hymenochirus* showed positive chemotaxis to water housing males with intact breeding glands, but females showed no reaction to water housing breeding gland-ablated males. Further, males showed no response to water housing either females or other males, indicating that the chemical cues are a female attractant, and not a signal geared towards males (i.e., neither a male repellent nor a species aggregation signal that attracts other male to a breeding site) (Pearl et al. 2000).

The presence of a mate-attraction chemical (Pearl et al. 2000), along with acoustic advertisement calls (Österdahl and Olsson 1963; Rabb and Rabb 1963; this study) suggests that *Hymenochirus* frogs use multiple sensory modalities in their reproductive behavior. To date the relative importance of chemical and acoustic signals is unclear, and we do not know whether either signal by itself, or a combination of both, is necessary for successful mate attraction and pair formation. It is possible that the chemical signal attracts the female to the breeding site, but that acoustic signals are subsequently used to localize males at the breeding site, or to choose among several males in the chorus. Conversely, calls could attract females to the chorus, and once there, females could use the chemical signal to choose among males.

The mate attraction efficacy of chemical and acoustic signals depends on water movement, microhabitat structure, and environmental background noise, as well as on the proximity of mate searching females. Variation in these environmental conditions may have played a role in the evolution of this multimodal communication system, and may still be important in determining the relative role each modality plays for mate choice. Although studies on multimodal communication in anurans have focused mainly on visual signals (Taylor et al. 2008; Starnberger et al. 2014), there are some examples of the use of vibrational (Lewis et al. 2001; Caldwell et al. 2010) and water-surface waves (Walkowiak and Münz 1985; Seidel et al. 2001; Höbel and Kolodziej 2013) to signal conspecifics. The uncommon (for anurans) use of chemical signals, combined with the small, yet complex vocal repertoire (complex call structure of the putative advertisement call, and probably graded aggressive call) suggest *Hymenochirus* frogs may be fruitful study subjects for examining the evolution of multimodal communication in anurans.

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Diet Composition of Southeast Asian Fanged Frogs of the *Limnonectes kuhlii* Species Complex

Post-metamorphic anurans are generally considered carnivorous, though some cases of frugivory and herbivory have been documented (Pertel et al. 2010). Various feeding strategies exist among anurans including sit-and-wait predation, active foraging, and opportunistic feeding (Duellman and Trueb 1986). Fanged frogs (Anura, Dicroglossidae) allied to the *Limnonectes kuhlii* (Tschudi 1838) complex are distributed throughout Southeast Asia and little is known about their feeding behavior and diet. Recent systematic work on this species complex has revealed that what was considered a single, widely distributed species for the past two centuries is actually a non-monophyletic group comprising more than 24 distinct evolutionary lineages (McLeod 2010). Several lineages occur in syntopy, and questions regarding niche partitioning are of particular interest in these cases.

Generally, frogs of the *L. kuhlii* complex are known to occur

primarily in riparian habitats and seem to be tied closely to these aquatic environments. Based on field studies of multiple species in Thailand, Malaysia, and Brunei, specimens are most frequently collected and observed sitting on the banks of streams, in shallow water at the edge of streams, in the shelter of boulders in high-flow stream conditions, or in lotic pond-like habitats associated with nearby streams. Rarely are individuals encountered in the forest habitat surrounding these aquatic environments. Unpublished data (DSM) suggests that these frogs are never more than 30 m away from water. Limited available information (McLeod 2009) and opportunistic observations (DSM) suggest that species of this complex may be sit-and-wait predators. One species, *Limnonectes megastomias* (McLeod 2008), was found to prey upon invertebrates, mollusks and even larger prey such as birds (McLeod 2009). The purpose of this work is to provide an initial assessment of the diet of different species of the *Limnonectes kuhlii* complex. Herein we document the diets (by way of gut content analyses) of 19 individuals representing nine species within the *L. kuhlii* complex.

Materials and Methods.—We analyzed gut contents from 19 specimens that were eviscerated for the purpose of producing osteological materials for use in another study. Specimens were collected in the field by a variety of people utilizing different methods of euthanasia, fixation, and preservation. In some cases individual animals were kept for only a few hours prior to euthanasia whereas in others individual animals may have remained in captivity without feeding for 12–24 h. Specimen data is presented in Table 1. Identified stomach contents are presented in Table 2. Lineage names follow those of McLeod (2010). Specimens examined and their respective gut contents

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