

Neighbor–Stranger Discrimination in Concave-Eared Torrent Frogs, *Odorrana tormota*

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Abstract

The dear enemy phenomenon in which animals discriminate familiar neighbors from unknown strangers, and respond more aggressively to strangers is well established in various social animals, especially in songbirds and mammals. So far, very few studies of neighbor–stranger discrimination have been carried out in amphibians and the results have been mixed. Thus, it is unclear whether this phenomenon exists commonly in frogs and toads, and whether it is exhibited by species with large vocal repertoires. We conducted acoustic playback experiments with male concave-eared torrent frogs (*Odorrana tormota*, a species with an unusually large vocal repertoire) kept in a tank in a quiet room to investigate whether or not they can discriminate strangers from neighbors acoustically. Nine of the 14 males tested showed evoked vocal responses to the calls from strangers, but none to calls from neighbors; vocal response to the calls from strangers was accompanied by aggressive motor activity. These results demonstrate that male *O. tormota* possess the ability to discriminate neighbors from strangers acoustically. *Odorrana tormota* therefore joins three ranid species (*Rana catesbiana*, *Rana clamitans*, *Rana dalmatina*, all known to have a comparatively small and stereotyped vocal repertoires) as the only anurans demonstrated to have this ability. Given the difference in signaling complexity between these frog species, the salient acoustic features used for discriminating neighbors and strangers are likely to be quite distinct.

Introduction

A variety of territorial animals (e.g., birds, mammals, lizards, fish, amphibians, and insects), especially those maintaining multi-purpose breeding territories, exhibit the ‘dear enemy phenomenon’ (see Temeles 1994; Briefer et al. 2008), in which they discriminate familiar neighbors from unknown strangers using a variety of sensory cues and respond more aggressively to strangers. By recognizing neighbors and respecting established territorial boundaries, individuals can conserve time and energy that would other-

wise be expended in unnecessary territorial defense (Falls 1982; Temeles 1994).

Sound communication plays an important role in the reproduction of anuran amphibians (Kelley 2004; Gerhardt & Bee 2007; Wells & Schwartz 2007). In most species, the male produces long-range advertisement calls that serve to attract mates and keep competitors at bay. Typically, a single male will begin to call at dusk, exciting nearby males to call leading to the formation of a chorus. All males call to out-signal their rivals to attract females, thus inter-male vocal interactions are intense and often

quite complex. Each male is behaviorally responsive to changes in local chorus density and to the approach of conspecifics (Wells & Schwartz 2007).

In amphibians, three ranid species with small vocal repertoires and stereotypic advertisement calls, American bullfrogs (*Rana catesbeiana*), green frogs (*R. clamitans*), and agile frogs (*R. dalmatina*), have been shown to display the dear enemy phenomenon (Davis 1987; Owen & Perrill 1998; Bee & Gerhardt 2001a,b,c; Bee 2004; Lesbarrères & Lodé 2002); they can use acoustic and location cues to discriminate neighbors which are accepted as 'dear enemies' from strangers that are attacked. In contrast, the Strawberry dart-poison frog (*Dendrobates pumilio*), which also has a small call repertoire comprised of stereotypic signals (Pröhl 2003), cannot discriminate strangers from neighbors acoustically (Bee 2003). Thus, at this time it is unclear whether the 'dear enemy phenomenon' is exhibited by anurans other than the three ranid species above, especially those with larger vocal repertoires. Song-bird species with medium or large repertoires have been suggested to have a reduced ability to recognize individuals (Kroodsma 1976; Falls 1982); whether or not this negative correlation between song repertoire and acoustic discrimination (i.e., the repertoire constraint hypothesis, *sensu* Kroodsma 1976) applies to anurans remains to be tested.

We carried out acoustic playback experiments with male concave-eared torrent frogs (*Odorrana tormota*; previously *Amolops tormotus*) in the laboratory to determine whether they can discriminate a stranger's call from a neighbor's call. *Odorrana tormota* represents an interesting test case because it has the largest vocal repertoire among anurans; their vocal signals are broadband containing spectral energy that extends into the ultrasonic range (Feng et al. 2002; Narins et al. 2004). One of the eight call-types of *O. tormota* (the long calls) shows pronounced frequency modulation and contains various non-linear phenomena [NLP: subharmonics, deterministic chaos (characterized by noisy signals that are not random noise, but are generated by a chaotic process within the vocal production system; Fitch et al. 2002), frequency jumps and biphonation] – these acoustic features vary greatly from one call to another within the same individual (Fig. 1; A.S. Feng, T. Riede, V. S. Arch, Z. L. Yu, Z. M. Xu, X. J. Yu, J. X. Shen, unpublished data). In spite of the extensive intra-individual variability, a quantitative analysis of long calls of marked frogs showed that males have consistent spectral and/or temporal call features that are individual specific; in particular, the average, maximum and minimum fundamental fre-

quencies, the call duration, and the durations of the subharmonic and chaotic segments of the frogs' long calls are individual specific. Moreover, individual males produce calls from their own calling sites (A.S. Feng, T. Riede, V.S. Arch, Z.L. Yu, Z.M. Xu, X.J. Yu, J.X. Shen, unpublished data) where male–female mating pairs (i.e., engaged in amplexus) can be found during the reproductive season (Shen et al. 2008), suggesting that these are multi-purpose breeding territories. Based on the possession of individually distinct calls and apparent defense of breeding territories, we hypothesized that *O. tormota* males display neighbor–stranger discrimination, despite having a large vocal repertoire of highly complex calls (Feng et al. 2002; Narins et al. 2004).

Methods

To assess whether male frogs possess the ability to discriminate neighbors from strangers on the basis of vocal signals, we performed acoustic playback experiments investigating the evoked vocal responses (EVRs) of male frogs kept in a plastic tank. The experiments were carried out between May 22 and 30 2006 (which corresponds to the mid-period of the breeding season of *O. tormota*), in Huangshan Hot Springs, China (30°06'N, 118°10'E). Experiments were performed between 20:00 and 24:00 h, within 48 h of capture. Prior to EVR tests, frogs were housed individually in 1-gallon transparent plastic bags in a room exposed to ambient light. The experimental protocol was approved by the Institutional Animal Care and Use Committees in the Chinese Academy of Science and the University of Illinois at Urbana-Champaign.

For EVR experiments, 14 male *O. tormota* from five acoustically isolated areas (2–4 frogs per area) were captured and placed in a transparent plastic tank (width × depth × height = 22 × 12 × 15 cm) which was setup indoors, approx. 1 km away from the frogs' natural habitat. The room was quiet and darkened. The top cover of the tank had slatted ventilating openings that facilitated sound transmission in and out of the tank. A Polaroid loudspeaker (diameter of 3.8 cm and a pass band of 22–120 kHz; roll-off: 10 dB/octave below 22 kHz) was attached to a tripod and placed ~12 cm above the tank. A computer-based playback system ('Play-unit'; Feng et al. 2006) broadcast the calls through the loudspeaker. A custom-made ultrasonic microphone with a frequency response of 15–120 kHz (roll-off: 6 dB/octave below and above this range) was mounted on a separate tripod and placed 10 cm above the

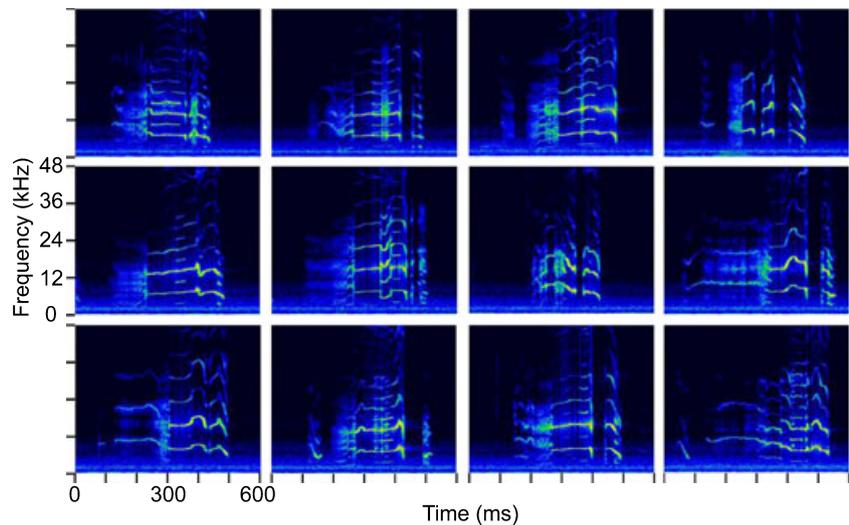


Fig. 1: Twelve representative long calls of a male *Odorrana tormota* showing the variability in the frequency modulation pattern and the time and frequency of occurrence of non-linear phenomena (chaos, frequency jumps and subharmonics). Shown are the sound spectrograms of these calls, which were derived using Selena, a custom-designed sound analysis software (Feng et al. 2006).

loudspeaker. This microphone was used to record the frog's vocal response as well as the acoustic playback stimulus. Recordings were made digitally with PCTape, a computer-based data acquisition system (Feng et al. 2006).

Calling sites of male *O. tormota* extend over a vast area of Huangshan Hotsprings, along the banks of the Tao-Hua Creek. Our study focused on frogs residing in five acoustically isolated areas (each is $<20 \times 20$ m); these areas are located at least 60–100 m apart and separated by bamboo forest and steep walls (>3 m in height) of man-made trails. Calls of a male from each area were recorded on May 20 and 21 at ambient temperature of 21–22°C, 60–75% humidity; afterward the calling sites were marked, and the calling frogs were captured and placed in a tank in a room separate from the experimental frogs. Of the eight call-types of *O. tormota* (A.S. Feng, T. Riede, V.S. Arch, Z.L. Yu, Z.M. Xu, X.J. Yu, J.X. Shen, unpublished data), long calls are the most intense with a peak sound pressure level of >100 dB SPL (A-weighting at 0.25 m), and are thus audible throughout each acoustically isolated area. We made systematic measurement of the attenuation of pure tones of 5–50 kHz in one of the study sites. The microphone was placed at various distances (1, 2, 4, 8, 16, and 32 m) from a loudspeaker broadcasting a series of tone pulses (100 ms duration) at 5, 10, 20, 30, 40, and 50 kHz; both the loudspeaker and microphone were at heights where frogs usually would vocalize. We recorded these signals on PCTape and analyzed their relative amplitude spectra using Selena, a custom-designed software program (see Narins et al. 2004). We found that the intensity of tone pulses was attenuated by 31–36 dB

at a distance of 8 m depending on tone frequency, and by an additional 20–24 dB at 32 m for tones up to 20 kHz (or 40–45 dB for tones >25 kHz). Therefore, calls emitted at the border of an acoustically isolated site would have a sound pressure level of >60 dB SPL at the opposite border – this is above the predominantly low-frequency ambient noise (peak energy at ~ 600 Hz ranges from 60 to 85 dB SPL) in the frequency range of calling and within the response range of midbrain auditory neurons in *O. tormota* (Feng et al. 2006).

Playback stimuli comprised a long call of a randomly selected male from each of the five areas. At nights when frogs were calling actively, we could find 10–20 frogs in each area. We define calls recorded from frogs occupying the same area (within 5–10 m away from the site of the calling male) as neighbor's calls, and those from frogs in remote areas as stranger's calls. The WAV files of the five long calls from the five different areas were stored on the Play-unit. The sound levels of these playback stimuli were equalized to ~ 75 dB SPL at the bottom of the test tank (A-weighting), approximating the SPL of a naturally calling frog at a distance of 2–4 m. During the playback experiment, each male was placed in the plastic tank and allowed 5 min for adaptation; the frog occasionally moved around the tank during the first 15–20 s of the adaptation period but became quiescent thereafter. It was then presented with three playback conditions (5-min period each with a 3-min break between trials): (i) a control period with no playback, (ii) a period during which a 'neighbor's' call (with respect to the subject in the tank) was presented at a rate of one call every 15 s, the approximate natural calling rate of the species, and (iii) a period during

which we presented a ‘stranger’s’ call at the same repetition rate. The order of playback presentation was randomized for each frog.

We quantified the number of calls produced during each of the 5-min test periods. During playback we additionally counted the number of responses occurring within ± 50 ms of the stimulus offset (defined as antiphonal responses). We performed a Friedman test to determine whether the numbers of calls produced in the three experimental conditions differ significantly. Subsequently, we made pair-wise comparisons using Wilcoxon’s signed rank test to determine whether the frogs’ evoked vocal response to the neighbor’s calls (EVR-N) differ significantly from the response to the unknown or stranger’s calls (EVR-S), and whether these EVRs differ from the frogs’ response during the control condition.

Results

Frogs’ behavior in captivity during the 5-min control period was uniform, and none vocalized in the absence of acoustic stimulation. Of the 14 males tested, five showed no differential EVRs to the calls of stranger and neighbor, i.e., these frogs did not respond, or responded equally weakly to both acoustic stimuli. For nine frogs, however, a stranger’s call produced marked EVR, eliciting multiple moderate to high level calls (75–106 dB SPL; A-weighting); these nine males gave no response to a neighbor’s call (Table 1). Friedman test (Table 2) showed that the calling activity in the three experimental conditions differed significantly (Chi square = 17.76; $df = 2$; $p < 0.001$). Pair-wise comparisons with Wilcoxon’s signed rank test (Table 3) showed that the frogs’ EVR-S (response to a stranger’s call) differed significantly from the control, as well as the EVR-N (response to a neighbor’s call).

There were additional differences in the frogs’ responses to neighbors’ and strangers’ calls. Notably, the majority of EVR-Ss were antiphonal responses, but few EVR-Ns were. Additionally, when presented with a stranger’s call (not a neighbor’s call), the frogs were restless and displayed various motor responses in the tank that reflected aggression toward the signal source, e.g., climbing the walls, and hopping and thrusting forward to the top cover of the tank.

Discussion

Results of the present study revealed that nine of 14 males (64%) from five acoustically isolated areas

Table 1: Evoked vocal responses of *Odorrana tormota* to a neighbor’s call (EVR-N) vs. a stranger’s call (EVR-S)

Frog #	Control	EVR-N	EVR-S
1	0	0	5
2	0	0	10
3	0	0	7
4	0	0	2 (2)
5	0	0	9 (6)
6	0	0	2 (2)
7	0	0	10 (7)
8	0	0	20 (17)
9	0	0	3 (1)
10	0	0	0
11	0	3	3
12	0	1	2
13	0	2 (2)	1 (1)
14	0	5	3

Shown are the number of calls produced during the control period (in the absence of acoustic playback stimulus) and the numbers of calls evoked by the respective playback stimuli during the 5-min test period. Numbers in parentheses represent frogs’ antiphonal responses occurring within ± 50 ms of the stimuli offset.

Table 2: Descriptive statistics of calling activity (number of calls produced) under the three experimental conditions

	n	\bar{x}	SD	Minimum	Maximum	Ranks
Control	14	0	0	0	0	1.39
EVR-N	14	.79	1.53	0	5	1.86
EVR-S	14	5.50	5.35	0	20	2.75

Friedman test showed that the calling activity in the three experimental conditions differed significantly (Chi square = 17.76; $df = 2$; $p < 0.001$).

Table 3: Pair-wise comparisons using Wilcoxon’s signed rank test showed that the EVR-S differed significantly from the EVR-N, and from the control

	EVR-N vs. Control	EVR-S vs. Control	EVR-S vs. EVR-N
Z	−1.83 ^a	−3.19 ^a	−2.63 ^a
Asymptotic significance (two-tailed)	0.068	0.001	0.008

^aZ values based on negative ranks.

effectively discriminate a neighbor’s call from a stranger’s call (Table 1). A neighbor’s call does not evoke these males to call, but when a stranger’s call is presented, it consistently elicits robust EVRs, the majority of which are antiphonal responses. Interestingly, this ratio of 64% closely approximates the result of discriminant functional analysis (DFA) of the long calls of *O. tormota* (A.S. Feng, T. Riede, V.S. Arch, Z.L. Yu, Z.M. Xu, X.J. Yu, J.X. Shen, unpublished data). DFA showed that on average 55% of

the long calls can be correctly assigned to individual frogs – while this is above the chance level it suggests a high degree of difficulty in discriminating individual calls, as reflected by a 64% success rate of neighbor–stranger discrimination.

The finding that not every male frog successfully discriminates a stranger's call from a neighbor's call is not surprising given that the vocal repertoires of *O. tormota* males are extraordinarily large. Each male can produce countless vocal signals – these show large variability in amplitude and frequency modulation patterns, and in the frequency of occurrence of various NLP (Fig. 1; Feng et al. 2002; Narins et al. 2004). In addition, the present discrimination experiments are challenging when compared to the discrimination experiments in previous studies (e.g., Falls 1982; Davis 1987; Temeles 1994; Bee & Gerhardt 2001a,b,c; Bee 2003). In those studies, the neighbor's call is that of the neighbor occupying immediately adjacent territories, and thus is most familiar to the test subject. In the present experiment, the neighbor's call is from a randomly selected male calling within a group of 10–20 frogs. While each male can hear the calls of other males within the group on most evenings during the reproductive season, the audibility is sometimes compromised when the ambient noise is intense, such as during a downpour. Finally, habituation has been proposed as a learning process leading to neighbor–stranger discrimination (Owen & Perrill 1998), which is likely also true for male *O. tormota* given the complexity and diversity of their vocal signals. Vocal learning takes time and thus the neighbor–stranger discrimination ability likely progresses over the course of a reproductive season. However, future research is necessary to determine the roles of learning in neighbor–stranger discrimination in *O. tormota* and whether the discrimination ability changes with time during its breeding season.

The neighbor–stranger discrimination ability of male *O. tormota* is comparable to that of male bullfrogs (Davis 1987; Bee & Gerhardt 2002). In the case of bullfrogs, males exhibit less aggression towards familiar neighbors at known calling sites (i.e., 'dear enemies'), compared to strangers' calls at the same sites or familiar neighbors at new calling sites. For this species, the location cue plays an important role. In contrast, discrimination in *O. tormota* is observed in a tank in a room, outside of the frogs' calling sites, and thus based on acoustic cues only without additional cues (e.g., localization cues).

Whereas the 'dear enemy phenomenon' in bullfrogs reflects inter-individual interactions, in

O. tormota it may represent inter-group competition. Namely, for *O. tormota*, individuals calling within an acoustically connected area are recognized as neighbors, and therefore part of the group, whereas those from distant, acoustically isolated areas are strangers who elicit an aggressive, territorial response. Our own observations in the field provide some support for this hypothesis: following acoustic playback of a stranger's call for 5 min; we often observe two to four males hugging the loudspeaker, apparently in an effort to challenge or chase away the 'intruder'. However, further experimentation is required to determine more definitively whether the 'dear enemy phenomenon' represents inter-individual or inter-group competition. Results of our playback experiments are similar to those of oscine birds (Briefer et al. 2008). Briefer and colleagues recently showed that skylarks, a territorial species with a large repertoire, display neighbor–stranger discrimination using distinct dialect features that are shared by all males in a bird's neighborhood (but do not exist in songs produced by males from separate geographical locations), i.e., group signatures. Whether or not vocal signals of male *O. tormota* carry group signatures is unclear – this is clearly a hypothesis worth testing.

At this time, the particular cues responsible for neighbor–stranger discrimination in *O. tormota* are unknown. In bullfrogs, although not experimentally validated, such discrimination seems to be based largely on small differences in the fundamental frequency (F0) of their vocal signals (Bee & Gerhardt 2002), and thus to differences in the physical properties of the vocal folds. For *O. tormota*, male vocal signals carry individual signatures (A.S. Feng, T. Riede, V.S. Arch, Z.L. Yu, Z.M. Xu, X.J. Yu, J.X. Shen, unpublished data). The individuals' long calls vary in terms of various linear and non-linear acoustic cues (comprising the average, the maximum and the minimum F0, the call duration, and the absolute and relative durations of the subharmonic and chaotic regimes). The relative contributions of these cues for neighbor–stranger discrimination remain to be determined. It is noted that, during our playback experiments, the F0 was markedly attenuated because of the frequency response of the loudspeaker. Thus, if the call spectrum was used to make neighbor–stranger discrimination frogs presumably relied on the second and/or third harmonics of the calls. It is likely that the frogs also rely on harmonics of the fundamental in their natural habitat given that the background noise is intense in the range of the call fundamental frequency.

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