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ORIGINAL PAPER

Socially mediated plasticity of chorusing behavior in the gladiator frog *Hypsiboas rosenbergi*

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Abstract Competition for mates often occurs in social settings composed of many displaying males. While this poses some special challenges for communication, the proximity of other males may also provide information that chorus participants may use to adaptively adjust their calling behavior to the local level of competition. Conducting behavioral observations in natural choruses as well as playback experiments with focal males, I investigated socially mediated plasticity in the calling behavior of a neotropical gladiator frog, *Hypsiboas rosenbergi*. In natural choruses, male call rate was negatively correlated with the distance to the nearest calling neighbor, suggesting that the presence and distance of competing males influences call rate in this species. In a playback experiment that tested for the effect of the presence and competitiveness of rivals, *H. rosenbergi* males proved able to quickly notice changes in their acoustic environment and to respond to those changes in a graded fashion. As competition increased (either by increasing the number or attractiveness of the simulated rivals), males raised their calling rate; as competition was reduced, males lowered their calling rate. This indicates that males can perceive changes in their social environment and modify their calling behavior in ways that reflect the level of competition in the chorus. This socially mediated plasticity in calling behavior may help males to economize their energy reserves.

Keywords Acoustic communication · Call rate · Call duration · Advertisement call · Playback trial · Evoked vocal response

Introduction

Competition for mates often occurs in social settings composed of many displaying males, such as leks or choruses (Andersson 1994). The highly competitive social environments created by the proximity of displaying rivals poses a range of challenges. For example, for organisms such as anurans and insects that rely on long-range acoustic communication for pair formation, interference from calls of nearby males, plus the general din created by the chorus as a whole, can interfere with mate recognition and localization (Gerhardt and Huber 2002; Wells 2007; Wells and Schwartz 2007). Despite these challenges, displaying in groups may also have benefits, because males may exploit the acoustic signals of groups of other males (a) to join those groups (Bee 2007; Swanson et al. 2007), (b) to adjust their own calling behavior (Wells 1988, and references therein; Byrne 2008), (c) to adjust their relative positioning within the chorus (Pfennig et al. 2000), or (d) to select the best times for displaying (Brooke et al. 2000; Byrne 2008). Further, males have lower predation risk in larger choruses (Ryan et al. 1981), and they may use call cessation of other chorus participants as an alarm cue to modulate calling activity (Dapper et al. 2011), thus reducing their own predation risk and energy expenditure.

Calling in frogs is one of the most energetically expensive behaviors of any vertebrate (Wells 2001, 2007), yet calling is also a crucial component of mate attraction in most species (Wells 2007). In playback trials, females generally prefer calls that are longer, faster, or louder (Ryan and Keddy-Hector 1992; Gerhardt and Huber 2002). Not surprisingly, male anurans often respond to elevated acoustic competition by increasing call intensity (Lopez et al. 1988; Bastos et al. 2011), call complexity (Schwartz 1986), call duration (Wells and Taigen 1986), or call repetition rate (Bosch and Márquez 1996; Benedix and Narins 1999; Tarano 2002). Such calls, however, are often more energetically costly to produce (Wells

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2001), and energetic constraints are expected to set a limit to the duration of nightly or seasonal calling. However, the best predictor of male mating success in anurans is chorus tenure, that is, the number of nights a male has participated in the chorus (Gerhardt et al. 1987; Murphy 1994; Höbel 2000). This suggests that male anurans are faced with a trade-off between short-term benefits accrued from exaggerated call traits and longer-term benefits accrued from increased chorus participation, favoring a mechanisms of adaptive energy allocation (Brepson et al. 2013). Socially mediated behavioral plasticity that allows males to track changes in the competitive environment may allow them to economize their energy expenditure, because they would not have to permanently maintain maximum calling effort, but only do so when the presence/attractiveness of other chorus participants requires it.

I tested three hypotheses that ask about the presence and extent of socially mediated plasticity in calling behavior in the neotropical tree frog *Hypsiboas rosenbergi*. (1) The hypothesis that male *H. rosenbergi* shows socially mediated plasticity in calling behavior predicts that variation in their competitive environment (i.e., chorus size, nearest neighbor distance, addition of competitors) will result in changes in their calling behavior. (2) The hypothesis that socially mediated plasticity maintains a male's competitiveness makes the prediction that males will match or exceed a competitors attractiveness. Finally, (3) the hypothesis that socially mediated plasticity in calling behavior is involved in adaptive energy allocation makes the prediction that males increase calling behavior when competition increases and decrease it when competition decreases. To test these hypotheses, I observed natural choruses of *H. rosenbergi* males for the relationship between male call rate, chorus size, and distance to nearest neighbor. I also conducted playback trials with focal males in the field, in which I simulated increasing/diminishing acoustic competition by varying the number of competitors as well as the level of their attractiveness.

Material and methods

Study species and study site

I studied the chorusing behavior of the gladiator frog *H. rosenbergi* from May to September 1995 at La Gamba Biological Station, Puntarenas Province, Costa Rica. Gladiator frogs are a clade of medium to large tree frogs (family Hylidae) that occur from Costa Rica into northern South America. The name gladiator frogs is a reference to their highly pugnacious behavior and well developed prepollical spine that they use when fighting. Most species of gladiator frogs build basins for egg deposition (see Höbel 2008 and references therein), and males do not start calling to attract females until they own a basin. Basin building constitutes a substantial investment by the males, since they spend from 30 min to several hours in constructing a basin (Kluge 1981; Martins 1993). Basin construction is often facultative, and whether males built their own basins or occupy suitable natural water-filled depressions depends on local habitat features. At my study site, choruses formed around a small swamp in the middle of a cattle pasture, and the presence of the cattle left the area littered with cattle footprints, many of which were filled with water (Höbel 1999, 2000). Males were perfectly capable of building their own basin (and did so in areas where cattle had no access), but most males (ca. 75 %) occupied basins originating from cattle footprints and puddles rather than building them (Höbel 1999, 2000).

Most anurans merely gather at suitable breeding sites and base decisions about spacing within the chorus on the perceived signal amplitudes of their neighbors (Brenowitz 1989). When a rival encroaches on the male's calling territory, he may relocate to another calling site (Brenowitz 1989). By contrast, male gladiator frogs exhibit a resource defense mating system, and because they only call from their basins, their calling sites are fixed (Höbel 2000). Males have to built a new basin, find a suitable natural basin to occupy, or take over the basin from another male before they can start to call (Kluge 1981; Höbel 2000). Consequently, they cannot quickly relocate to a different calling site when confronted with acoustic competition. Given the spatial limitations of their calling sites within a chorus, male gladiator frogs should be particularly sensitive to changes in their acoustic environment and show behavioral plasticity to mediate social competition.

The calls of males from this population typically consist of two short notes (see Fig. 4a), but males sometimes produce calls with three or even four notes (Höbel 2000). The production of three- and four-note calls is associated with increased male-male competition, as they are more frequently given when males are calling close to each other (per. obs.) or during playback experiments in which a male is confronted with a conspecific call broadcast at higher amplitudes (>85 dB; unpubl. data). Average chorus size in the study population was 16±6 males (range 1–25), and average nearest neighbor distance was 8.4±6.6 m (range 1.5–55 m; Höbel 2000).

Observations of natural chorusing behavior

Given the range of nearest neighbor distances (up to 55 m; Höbel 2000) and difficulty of terrain, simultaneous recording of calls of nearest neighbor males was not feasible. To examine socially mediated plasticity in calling behavior of undisturbed males, I therefore focused on call repetition rate by counting the number of calls a male emitted during 1 min (with the help of a stopwatch).

On 20 nights, I obtained call rate counts (n=125 1-min counts); dates and times for the counts were spread across the breeding season and across the times of nightly calling activity

(1800–2300 h local time). During each of the sampling nights, I counted call rates of on average (±SD) 6±4 (range 1–14) males, sampling each male only once. I also noted the time of night at which the counts were taken, the size of the chorus (number of calling males), and the distance to the nearest calling neighbor (nearest neighbor distance). I used this data to ask whether call rate is related to time of night, chorus size, or nearest neighbor distance. On 8 nights, I counted the call rate of males that were each other's nearest neighbors (n=21 nearest neighbor pairs), which allowed for a more detailed comparison between the call rates of these males. I used those counts to ask whether nearest neighbor males match their call rate to each other. Although I cannot rule out that some males were counted more than once, I think the potential for repeatedly measuring the same male was very low because of the size of the area and the short chorus tenure (3 nights; Höbel 2000) relative to the time span over which the counts were taken.

Experimental manipulation of chorusing environment

To test how calling behavior is influenced by changes in their social environment, I conducted playback experiments in which I simulated the addition of acoustic competition by broadcasting synthetic advertisement calls to calling males in the field. I generated two different synthetic stimuli modeled after *H. rosenbergi* advertisement calls (Höbel 2000): one was modeled after the typical two-note advertisement call (2 N), the other after a more attractive four-note call (4 N; Fig. 1). Results of preliminary trials testing preferences of female gladiator frogs indicate that they tend to prefer higher number of notes in a call (4 N over 2 N, and 2 N over 1 N; Höbel, unpubl.). I presented those stimuli to 10 focal males.

Stimulus generation

To create the call stimuli, I used a 1390-B Random Noise Generator and several parallel frequency filters (Krohn-Hite 3500; Rockland Model 825 Dual Hi/Lo filter) to generate noise in the frequency range of a *H. rosenbergi* advertisement call. The resulting sound had a frequency range of 0.2–2.9 kHz, with emphasized frequencies at 0.3–0.6 and 1.1–1.3 kHz. Then, I used a pulse generator (Zeits Instruments Max 21-stimulator) to produce stimulus segments of desired length (50 ms; rise-fall time of 5 ms; equivalent to one call note), which I then combined into two (2 N) and four (4 N) note groups (inter-note interval of 75 ms) to create the actual call stimuli. The 2 N call stimulus therefore had a total duration of 175 ms, and the 4 N call stimulus had a total duration of 425 ms. The two call stimuli (2 N and 4 N, respectively) were recorded on different channels of a cassette tape at a rate of 36 call stimuli per minute. Both call stimuli exactly alternated with each other. Note duration, inter-note interval, and overall call duration of these stimuli were close to the average values found in the study population (Höbel 2000). The call rate of these call stimuli was within the low range of call rates observed in the study population (Höbel 2000).

To calibrate stimulus amplitude, I marked which gain settings on the playback recorder corresponded to 85 dB SPL at the distance of 2 m of each of the two experimental stimuli, using an BandK Type 2636 sound level meter with a BandK 4135 microphone in a sound-attenuated room. During field trials, I used a measuring tape to position the speakers exactly 2 m from the focal male. Control trials in the sound-attenuated room showed that playback amplitude was reproducible using this procedure with a margin of error of ±2 dB.

Playback procedure

I selected focal males based on large distance to nearest neighbor and consistent calling activity. I carefully placed a microphone mounted on a tripod over the basin of the focal male and positioned two speakers, each at a distance of 2 m from the basin. To ensure that the focal male perceived the stimuli as originating from two different neighbors, I placed the speakers at angles between 90° and 180°, depending on

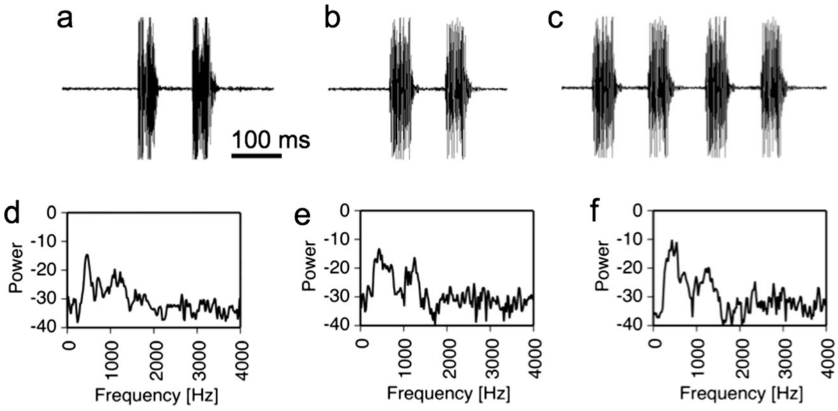

Fig. 1 Call of *Hypsiboas rosenbergi* (**a**, **d**), and 2 N (**b**, **e**) and 4 N (**c**, **f**) stimuli used in the experiments. Waveform (*top row*) and power spectrum (*bottom row*)

local topography and vegetation. The experimental stimuli were played back with a Phillips D6920MK2 Stereo cassette recorder and a Visaton FSR 10 WP speaker and the vocal response of the male was simultaneously recorded with a Sony WM-D6C recorder and a Sony ECM 969 microphone.

A complete set of trials lasted 15 min and consisted of five 3-min segments. I first recorded the calls of the focal male during a 3-min pre-stimulus period (PRE). Then, I started to broadcast the 2 N stimulus from one speaker for 3 min while simultaneously recording the vocal response of the male. After 3 min, I added the 4 N stimulus by switching on the second speaker, thus confronting the focal male with two calling neighbors (2 N+4 N). After another 3 min, I stopped the playback of the 2 N stimulus, thus reducing the playback to the 4 N stimulus only. Finally, I stopped the playback of test stimuli altogether and recorded a 3 min post-stimulus period (POST).

Call analysis

I digitized the recordings at a sampling rate of 22.5 kHz and used the program CoolEdit96 (Syntrillium Co.) to measure the following call properties: (1) the call rate, that is the number of calls given each minute; (2) the call duration, measured from start of the first note to end of second note; (3) the inter-note interval, measured as the time from end of the first note to beginning of second note; and (4) the note duration, measured from the onset to the offset of each note. I measured every advertisement call given during the experimental period and calculated averages for each minute. This allowed me to also test how quickly males changed their calling behavior in response to playback stimuli.

Statistical analysis

To examine what affects call rate in natural choruses, I used a mixed model (Standard Least Squares; REML). This test provides P values for fixed factors and confidence intervals for random factors. Confidence intervals overlapping zero indicate non-significant effects. I entered a call rate as a response variable, and nearest neighbor distance, chorus size, and time of night as fixed factors. I accounted for variation in climatic conditions between observation dates by entering date as a random effect in the model. To compare whether males adjust their call rate to that of their nearest neighbor, and whether the difference in call rate between nearest neighbors is affected by the distance between them, I calculated Pearson correlations.

To test the effects of playback stimuli on male calling behavior, I also used a mixed model (Standard Least Squares; REML). I ran separate tests for each of the four call traits I had measured in the experimental animals (call rate, call duration, inter-note interval, and note duration, respectively). I entered the respective call property as a response variable (i.e., call rate), and treatment (i.e., silent controls or playback stimuli) and minute nested within treatment (1st, 2nd, or 3rd minute of each playback treatment) as fixed factors. I included male identity as a random term in all models because each male's responses was measured to multiple treatments. Because the mixed models only provide information about whether treatments did differ in effect, not how they differed, I additionally used LSMeans differences Student's t tests to compute pairwise comparisons between different treatments. All statistical analyses were performed with JMP 8.0.1 (SAS Institute, Cary, NC, USA).

Results

Observations of natural chorusing behavior

In natural choruses, call rate increased with decreasing nearest neighbor distance ($F_{1,102.7}=7.41$, $P=0.008$; Fig. 2a) but was unaffected by chorus size ($F_{1,46.75}=1.14$, $P=0.29$, Fig. 2b). On average, call rate was highest after nightfall (1800 h local time) and then decreased toward the end of the night ($F_{16,102.6}=12.56$, $P=0.0006$, Fig. 2c).

Nearest neighbor males that were counted within 1 min of each other had similar call rates (Pearson correlation $r=0.71$, $P=0.0002$; Fig. 3a), suggesting that nearest neighbor males adjust their call rate to each other. Call rate adjustments were independent of nearest neighbor distance (Pearson correlation $r=0.19$, $P=0.34$; Fig. 3b), suggesting that the presence of the rival male is more important than his proximity.

Experimental manipulation of chorusing environment

During playback trials, males reacted to changes in acoustic competition by changing their call rate (Table 1, Fig. 4a). The addition of two males (2 N and 4 N stimuli) and addition of one attractive male (4 N stimulus) resulted in an increase in call rate in the focal males. By contrast, the addition of one male of average attractiveness (2 N stimulus) did not have much effect on a focal male's calling behavior. Males responded very fast to an increase in competition (effect already visible in the first minute of each playback treatment; Table 1), and they responded just as fast to the reduction in competition by lowering their call rates (Table 1).

Males also modified their fine temporal call properties in response to changes in their acoustic environment; males increased call duration and inter-call interval in response to increased competition (Table 1; Fig. 4b, c). There were two interesting patterns of socially mediated call modification. First, call duration and inter-note interval remained elevated even after the playback ceased (Fig. 4b, c). Second, males did

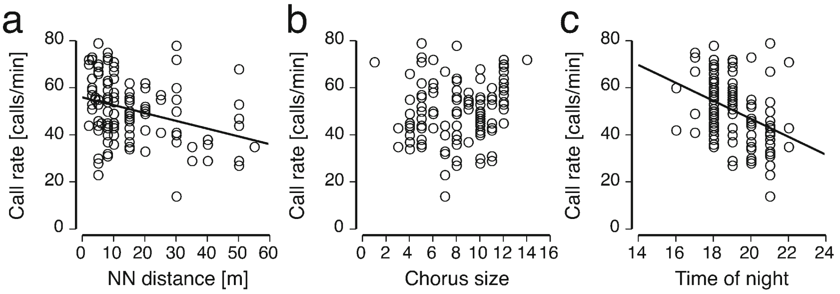

Fig. 2 In natural choruses, call rate of *H. rosenbergi* males is related to the distance to their nearest neighbor (**a**), not related to overall chorus size (**b**), and highest during the first part of the night (**c**)

not change the duration of the notes that comprise the call (Table 1; Fig. 4d); consequently, the increase in call duration was mainly a function of the longer inter-note interval, and longer call duration does not equal higher energy content because note duration remained constant.

Discussion

Both observational data linking chorusing behavior to natural variation in social competition, as well as experiments manipulating the degree of social competition faced by focal males, supports the hypotheses (1) that males of *H. rosenbergi* tree frogs show socially mediated plasticity in calling behavior, (2) that plasticity in calling behavior maintains a male's attractiveness in the face of competition, and (3) that plasticity in calling behavior may be involved in adaptive energy allocation.

In natural choruses, the call rate of *H. rosenbergi* males was associated with the distance of its nearest neighbor, and during playback trials, males tracked an increased or decreased of vocal competition by changing their call rate, their call duration, and their inter-note interval. This behavior is consistent with reports from other anuran species, which also alter calling behavior under experimentally modified competitive conditions and generally show the strongest behavioral change involving call rate (Wells and Greer 1981; Benedix and Narins 1999; Bosch and Márquez 1996; Bastos et al. 2011; Tarano 2002).

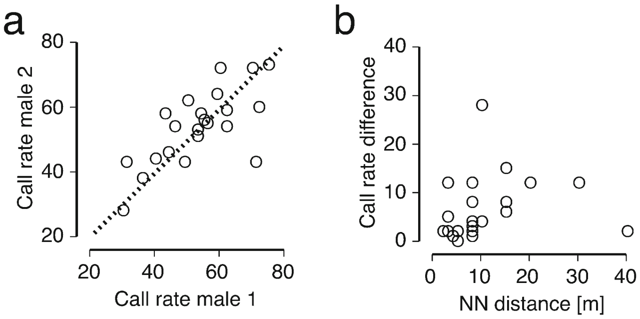

Fig. 3 In natural choruses, the call rate of *H. rosenbergi* males that are each other's nearest neighbor is similar (**a**) but not a function of the distance between the neighboring males (**b**). The *dashed line* in **a** denotes the 1:1 match

Male's responses to increased competition can show two basic forms: (a) a fixed response to competition, where the behavior changes but the change is not correlated to the characteristics of the competitor, or (b) a graded response where the level of behavioral change is a function of the characteristics of the competitor. Both types of responses can be found in anuran amphibians. For example, male túngara frogs (*Physalaemus pustulosus*) increase call complexity (by adding chucks notes to their calls) in response to complex calls versus simple calls, but there is not much difference in response to playbacks of calls with one or many chucks (Bernal et al. 2009). And male *Eleutherodactylus coqui* and *Physalaemus enesefae* increase call rate in response to playbacks, but this increase does not follow or match the rate of increase of the presented stimuli (Benedix and Narins 1999), or differs between stimuli of varying attractiveness (Tarano 2002). On the other hand, *Dendropsophus microcephalus* tree frogs increase call complexity in response to stimulus complexity (Schwartz 1986). Similarly, *Alytes cysternasii* midwife toads increase call rate more when interacting with playbacks with attractive features (low frequency, high rate; Bosch and Márquez 1996), and *Hyla versicolor* tree frogs give longer

Table 1 Results of Standard Least Squares model testing the effect of treatment and minute (within treatment) on call properties of *Hypsiboas rosenbergi*

Call property	Source	*DF*	*F* ratio	*P* value
Call rate	Treatment	4,123.1	5.69	*0.0003*
	Minute [treatment]	10,123	0.42	0.94
	Male and random			*Not overlap 0*
Call duration	Treatment	4,123	6.19	*0.0001*
	Minute [treatment]	10,123	0.89	0.55
	Male and random			*Not overlap 0*
Inter-note interval	Treatment	4,123	6.73	*<0.0001*
	Minute [treatment]	10,123	0.96	0.48
	Male and random			*Not overlap 0*
Note duration	Treatment	4,123	1.97	0.104
	Minute [treatment]	10,123	0.11	0.99
	Male and random			*Not overlap 0*

Significant terms are set in italics

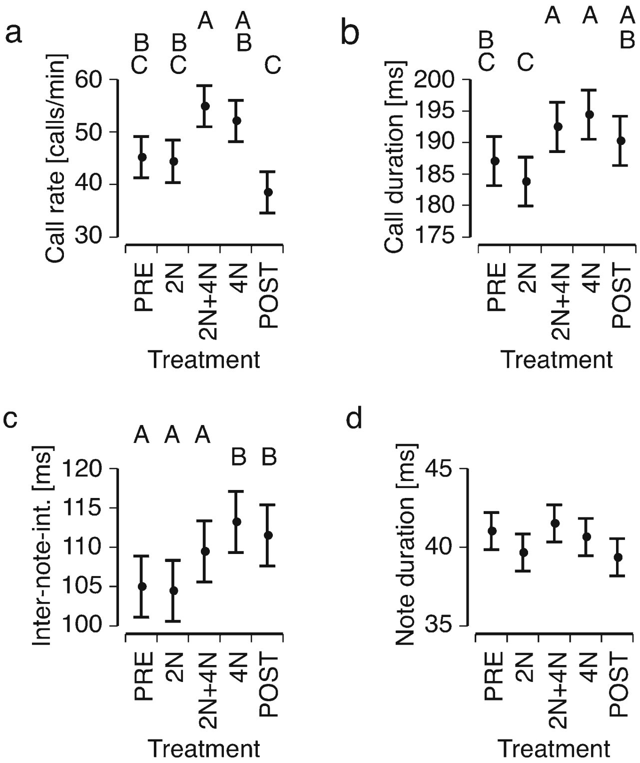

Fig. 4 Change of calling behavior of *H. rosenbergi* males in response to playback treatments simulating acoustic competition (plus the PRE and POST silent control periods). **a** Males increase call rate in response to high competition (2 N+4 N, 4 N) but reduced it once the competition disappears; **b** they increase call duration in response to high competition and maintain it after competition disappears; **c** they increase and maintain long inter-note intervals as the number of long (4 N) stimuli increase; **d** they do not modify note duration. Shown are mean (±SE) call properties; significant differences between treatments are illustrated with *letters* above the symbols (computed with LSMeans Differences Student's t tests)

calls in response to attractive long calls or to stimuli presented at high rates (Wells and Taigen 1986). The *H. rosenbergi* males investigated here also showed a graded response: the 2 N stimulus elicited almost no response, but call rate was elevated in the 2 N+4 N and 4 N treatments.

What is noteworthy is that graded responses to vocal competition rarely take the form of an exact matching of calling performance (Gerhardt et al. 2000a), but rather track stimulus variation without exactly matching it (Schwartz 1986; Wells and Taigen 1986; Bosch and Márquez 1996). Yet, even this imperfect tracking may be sufficient to equalize attractiveness between neighboring males, and the energy expenditure required to exceed a rival's attractiveness may yield limited returns. This is because female discrimination thresholds are frequently surprisingly large (Gerhardt et al. 2000b; Rosso et al. 2006). Consequently, having a slightly lower call rate than the neighbor may be sufficient to be perceived as equally attractive by the female, while increasing call rate to the point where the female can discriminate among males may not be energetically feasible. Further, in both *H. rosenbergi* and *Hyla microcephala* (Schwartz 1986), data obtained from natural observations showed a closer correspondence between the calling behavior of neighboring males than data obtained during playback experiments. While I did observe a correlation between the call rates of nearest neighbors in natural choruses, males did not match call rate during playback trials. The rate of the playback stimuli used in the trials (36 calls/min) was lower than the undisturbed call rate of most focal males (range 33–57 calls/min). Maybe males do not match the call rate if they have to substantially lower their own rhythm to do so. Then again, some of the matched nearest neighbor pairs in the chorus did call in the range of 35 calls/min, which would suggest that the playback call rate was not unnaturally slow. Maybe males need longer periods of time (i.e., more than 3 min of playback) for call matching to be achieved.

Was the graded response observed in *H. rosenbergi* due to an increase in the number of rivals (1 to 2) or to an increase in the number of call notes the males perceived (2, 6, 4)? Because I did not have a 2 N+2 N treatment (i.e., four notes from two different sources) and did not switch the order of presentation (i.e., sometimes start with the 4 N instead of the 2 N stimulus), it is impossible to tease those two possibilities apart. However, call rate was more similar during the 2 N+4 N and the 4 N treatments compared to the 2 N treatment, suggesting that they may pay closer attention to the relative attractiveness of acoustic competition than to the number of competing rivals (both 4 N and 2 N stimuli represented one rival male). Few studies have investigated the importance of the number of potential rivals on male calling behavior, but Schwartz et al. (2002) found that in staged choruses, male *H. versicolor* tree frogs were sensitive to the addition and removal of chorus participants, and often responded to changes in group size with changes in call duration and call rate.

Males not only increased call rate when confronted with an increase in competition, but they also showed an even stronger decrease in call rate when competition decreased. Exaggerated reduction of calling effort after the offset of playback treatments is not universal but has been observed in several other species (Arak 1983; Given 1993; Giasson and Haddad 2006), suggesting that males may be even more sensitive to the reduction of vocal competition than to an increase (see also Goutte et al. 2010). Responding to decreased acoustic competition by quickly and strongly decreasing call effort may be a good strategy to save energy. Alternatively, some males may already be calling near their upper limit, and any change tracking increased competition may be less marked than a change tracking decreased competition.

Frequently, longer calls are equivalent to higher energy output, because call duration is increased by prolonging single note calls or adding pulses to pulsed ones (Taigen and Wells 1985). In present study, increased call duration was mainly a function of a longer inter-note interval, while note duration remained constant. This results in a longer call without increased energy content, suggesting that the increase in call duration observed during the 2 N+4 N and 4 N treatments probably does not function in increasing call attractiveness when faced with competition. Rather, increased call duration may be an artifact of males prolonging the inter-note interval in an effort to avoid overlapping their call notes with the 4 N stimuli. Females frequently discriminate against overlapped calls, and call timing, where males place their own calls relative to those of nearby individuals in an effort to avoid call overlap, is a commonly observed behavior among communally signaling animals (Greenfield 1994; Höbel and Gerhardt 2007).

The vast majority of studies documenting alteration of male calling behavior under competitive conditions do so employing experimental manipulation (generally playback trials, see above), while fewer studies also document similar responses in naturally behaving animals (Arak 1983; Bastos et al. 2011; Toledo and Haddad 2005). On the one hand, the general match between results from observational and experimental studies suggests that playback trials are good mimics of acoustic competition and can provide a window into how calling males experience and respond to social competition. On the other hand, the observation that the correspondence of calling behavior is generally tighter during natural interactions compared to playback experiments (Schwartz 1986; this study) suggests that the generally short duration time of playback treatments (1–3 min; Ryan and Rand 1998; Giasson and Haddad 2006; Tárano and Fuenmayor 2009; Bastos et al. 2011) may not capture all behavioral adjustments that occur during natural interactions. Given that nightly chorusing often last several hours, significantly increasing the duration of playback treatments may lead to new insights into the behavioral responses of male anurans to social competition.

Finally, the documentation of socially mediated changes in calling behavior provided by this and other studies (i.e., Wells and Taigen 1986; Bosch and Márquez 1996; Benedix and Narins 1999; Tarano 2002) is consistent with the hypothesis that plasticity in calling behavior may be involved in adaptive energy allocation mediating the trade-off between short-term relative attractiveness vis-a-vis a nearby neighbor and longer-term effects on reproductive success via increased chorus tenure. Indeed, studying the effect of energy constraints on calling behavior of the tree frog *Hyla arborea*, Brepson et al. (2013) recently documented the existence of such a trade-off between maintaining call features conferring short-term attractiveness or long-term nightly calling activity, and found that males of different conditions opted for different allocation strategies. However, to my knowledge, no study has yet demonstrated that males that adjust their calling behavior, or those that do it better or faster, actually increase their chorus tenure or their reproductive success. This may be a worthwhile topic for future studies.

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