



## Original Article

# Competitively mediated changes in male toad calls can depend on call structure

Rebecca Stirman and Karin S. Pfennig<sup>\*</sup>

Department of Biology, University of North Carolina, CB#3280, South Road, Coker Hall, Chapel Hill, NC 27599-3280, USA

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Males of many species aggregate in large groups where they signal to attract females. These large aggregations create intense competition for mates, and the simultaneous signaling by many individuals can impair any given male's ability to attract females. In response to this situation, male signals can be modified, either evolutionarily or facultatively, such that the detectability of the signal is enhanced. The way in which signals are modified varies among even closely related species, yet few studies have evaluated what causes such variation. Here, we address this issue using male spadefoot toads (*Spea multiplicata* and *Spea bombifrons*), which call to attract females. Using data from natural populations, we examined if, and how, male calls of 3 different call types (*S. multiplicata* with a slow call, *S. bombifrons* with a slow call, and *S. bombifrons* with a fast call) varied depending on competition with other males. We found that in both call types consisting of slow calls, call pulse rate decreased with increasing competition. By contrast, in the call type consisting of fast calls, call rate decreased with increasing competition. Moreover, we found that the relationship between competition and male call effort—a measure of the energy that males expend in calling—differed between the call types. Such variation in male signals in response to competition can have important implications for explaining diversity in male signals and patterns of sexual selection.

**Key words:** hybridization, male–male competition, mate choice, neighbor effects, reproductive interference, sexual selection.

## INTRODUCTION

Males across a diverse range of species and signal modalities aggregate in large groups, where they signal to attract mates (Emlen and Oring 1977; Greenfield 2005). These dense aggregations present males with a challenging environment. Competition for mates can be intense, and the number of simultaneously signaling males generates interference among male signals (Greenfield 1994; Wiley 1994; Brumm and Slabbekoorn 2005; Greenfield 2005). Such interference can impair a male's ability to assess his competitive environment (Schwartz 1987), prevent females from effectively evaluating a given male's signal (Wollerman 1999; Wollerman and Wiley 2002), and/or reduce the attractiveness of a male's signal (Schwartz and Wells 1983; Legendre et al. 2012). Males at breeding aggregations are thus under strong selection to produce signals that stand out in noisy signaling environments while also being successful in male–male competitive interactions and mate attraction (Wiley 1994; Brumm and Slabbekoorn 2005).

This selection can lead to evolutionary changes in male signals (Wiley 1994; Brumm and Slabbekoorn 2005), or, alternatively, it might favor males that facultatively modify their signals in response to the competitive environment (Klump and Gerhardt 1992; Brumm and Todt 2004; How et al. 2008; Reichert 2011; Reichert and Gerhardt 2012). Regardless of whether male signals are modified evolutionarily or facultatively, 2 features of the competitive signaling environment potentially impact male signals. First, male signals may be influenced by the overall noise level of the aggregation, which is dependent on total numbers of males (Wiley 1994; Brumm and Slabbekoorn 2005). Second, males might respond to the signals of their nearest neighbors, which constitute their closest competitors (Gerhardt and Klump 1988; Brush and Narins 1989; Schwartz 1993), and potentially interfere most directly with a male's signals.

Signal adjustments add a layer of complexity to sexual selection because the distribution of male traits from which females choose can depend on both the signaling environment and the ways in which male signals are modified (evolutionarily or facultatively) in that environment (Greenfield 2005). This becomes particularly important if the aspects of male signals that are modified are also those that indicate male quality or species identity to females (Halfwerk et al. 2011). Additionally, signal modification can cause males to invest greater energy in signaling (Prestwich 1994; Brumm

Address correspondence to: K.S. Pfennig. E-mail: kpfennig@unc.edu  
R. Stirman is now at Department of Fish and Wildlife Conservation, Cheatham Hall, RM 101 (MC0321) 310 West Campus Drive, Virginia Tech, Blacksburg, VA 24061, USA

and Todt 2004), which can increase the already high cost of signal production. Changes in signaling costs can, in turn, alter how long males can spend signaling and/or their ability to attend multiple breeding aggregations (Greenfield 1994; Murphy 1994).

Interestingly, competitively mediated changes in male signals vary between even closely related species. For example, in anurans, one species might alter call rate in response to reproductive interference from competitors (Wagner 1989), whereas another species might alter pulse rate (Martinez-Rivera and Gerhardt 2008). One explanation for this variation is that it could represent species-specific patterns of selection on optimal male signaling (Wiley 1994). Although for one species a given signal modification might make males more attractive to females (Reichert 2011, 2012), in a different species, the same modification might make males unattractive. This differential selection could, in turn, cause variation in signal modification across species.

A further explanation for variation in male responses to noisy, competitive environments is that signal structure itself determines the best strategy of signal adjustment (Grafe 2003). In other words, for a given species, the properties of the signal they produce might determine the most effective signal modification strategy for outcompeting other males, reducing the effects of reproductive interference, and attracting females. In the case of anurans, for example, changes in pulse rate might best enable males of one species to minimize the impacts of overlapping signals with competing males, whereas in another species in which pulse rate is not readily altered, changes in call rate might be more effective. Thus, signals that maximize male competitiveness or attractiveness will be favored by selection (Wiley 1994; Bradbury and Vehrencamp 1998; Brumm and Slabbekoorn 2005), but the modifications to an existing signal that enhance its efficacy could depend on existing signal structure and how it interacts with the noisy, competitive environment (Greenfield 1994; Greenfield 2005).

We evaluated this hypothesis using Mexican spadefoot toads (*Spea multiplicata*) and Plains spadefoot toads (*Spea bombifrons*) as our study system. Our goals were 2-fold. First, we ascertained whether aspects of males' calls varied depending on their competitive environment. Second, we asked if males of 3 structurally different call types (see Methods below) differed in how competitive environment affected their calls. Although our comparison was limited to 3 groups, our

results are consistent with the possibility that signal structure can impact competitively mediated changes in male sexual signals.

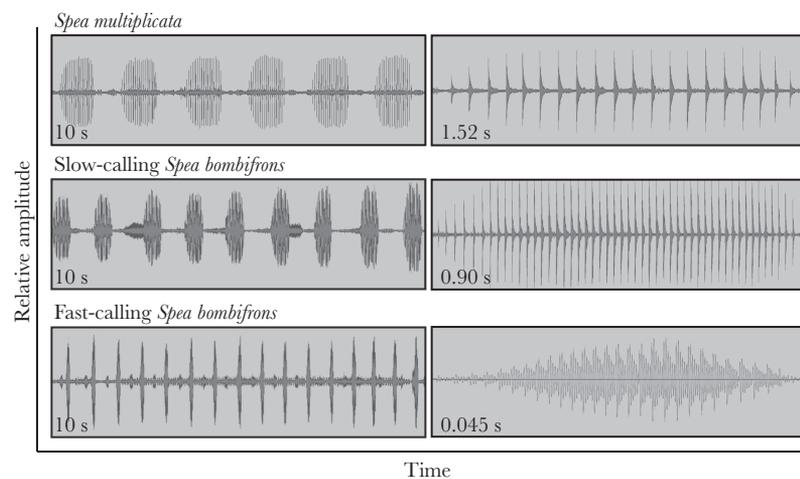
## METHODS

### Study system

Mexican spadefoot toads (*S. multiplicata*) and Plains spadefoot toads (*S. bombifrons*) are congeners that co-occur across a large portion of their ranges (Powell et al. 2016). Both species are explosive breeders that share breeding sites in ephemeral ponds that form after heavy rains (Pfennig 2000). Aggregations of males can be large and competition for mates intense (Simovich 1985; Sullivan and Sullivan 1985). Females choose males from among the aggregation and males can greatly outnumber females (Sullivan and Sullivan 1985; Pfennig 2000). Moreover, males call for at most a few days per year and in some parts of their range, they call for only a single night (Bragg 1965). Because of this, opportunities for males to mate successfully are limited. Consequently, spadefoot males are likely under strong selection to produce calls that are both readily detected and preferred by females.

*Spea multiplicata* and *S. bombifrons* produce calls that are distinct from one another throughout their ranges (Figure 1), and within *S. bombifrons*, males produce 2 distinct, geographically distributed, call types (Pierce 1976). Throughout the Great Plains of the USA and Canada, *S. bombifrons* produce a “slow call” type, whereas in southeastern Arizona and southern New Mexico, *S. bombifrons* produce a “fast call” type (Pierce 1976). Of the 3 male types (*S. multiplicata*, slow-calling *S. bombifrons*, fast-calling *S. bombifrons*), *S. multiplicata* calls are the slowest, with longer call durations, slow call rates, and audible space between pulses (Figure 1). The slow call type of *S. bombifrons* is slightly faster than the call of *S. multiplicata* with a shorter duration, faster call rates, and less separated, though still distinct, pulses. The fast call type of *S. bombifrons* is the fastest of the 3 with very short calls, rapid pulse rates with unseparated pulses, and short intercall intervals (Figure 1).

We determined whether and how males of each call type respond to the noisy, competitive environment of breeding aggregations. To describe the signaling environment, we measured both the total number of calling *Spea* males in the pond (“total



**Figure 1** Waveforms of *S. multiplicata* (top), slow-calling *S. bombifrons* (middle), and fast-calling *S. bombifrons* (bottom). Left panels: a 10-s call series for each male type; right panels: a single call for each male type.

*Spea*) and the distance from a focal male to the nearest calling male (“nearest neighbor”). Together, these 2 parameters provided measures of the noisy signaling environment that a male might experience from competing males in the aggregation. The “total *Spea*” measure provided us with an indication of the general background noise level from conspecifics, which can interfere with signaling (Schwartz 1993; Grafe 1996; Martinez-Rivera and Gerhardt 2008), whereas the distance to the “nearest neighbor” measure indicated the potential for direct interactions with a male’s closest competitor (Greenfield 2005). In anurans, females can find it difficult to distinguish between males calling close together (Farris et al. 2002), and previous research has shown that spatial separation can be a key component to successfully discriminating males (Schwartz and Gerhardt 1989). Indeed, research in other anurans shows that males attend most closely to their nearest neighbors in competitive interactions (Gerhardt and Klump 1988; Brush and Narins 1989; Schwartz 1993), though this is not always the case (Greenfield and Rand 2000).

### Field collections

We recorded 358 spadefoot toads from 43 different populations during the spadefoot breeding seasons of 2016 and 2017. Recordings were collected on an iPhone 4 using the Recorder Plus app (version 2.7.1) by Turbokey Studio. The simplicity of *Spea* calls meant this device was capable of recording calls with sufficient quality for our needs. These populations were located throughout Texas, Colorado, Kansas, New Mexico, and Arizona. At each pond, we estimated the total number of calling *Spea* and then recorded a selection of calling males for a minimum of 12 s at a sampling rate of 44.1 kHz. For a subset of the recorded males (85 slow-calling *S. bombifrons*, 24 fast-calling *S. bombifrons*, and 43 *S. multiplicata*), we also estimated the distance from the focal male to the nearest calling male. These were drawn from 26 populations located in Texas, Colorado, Kansas, and New Mexico. Of the 358 recorded males, we caught, weighed, and measured 207 males. From each of these males, we also obtained a tissue sample for subsequent genetic validation of species identification (see “Genotyping” below).

### Call analysis

We analyzed each male’s call to determine call rate (calls/minute), pulse rate (pulses/second), call duration (seconds), and call effort (total time spent calling/minute) using Audacity sound analysis software 2.1.3. Dominant frequency (Hz) was measured using Raven Pro 1.5 software. We used a fast Fourier transformation with a hamming window, a hop size of 82, and a Discrete Fourier Transform of size 2048.

### Genotyping

*Spea multiplicata* and *S. bombifrons* hybridize, and hybridization can influence call characteristics (Pfennig 2000). To ensure that the presence of hybrids did not influence our results, we genotyped each toad we were able to catch (a total of 166 males), and then removed any putative hybrids from the entire call data set using the following methods.

For those males from which we were able to obtain a tissue sample, we determined their species identity using a suite of 9 nuclear markers and 1 mitochondrial marker following Pfennig et al. (2012). We combined our data with previously collected data on call parameters and genotypes (this included an additional 58 fast-calling *S. bombifrons*, 167 slow-calling *S. bombifrons*, 42 *S. multiplicata*,

and 3 hybrids) and performed a principal component analysis (PCA) using the standardized values of call rate, pulse rate, dominant frequency, and pulse number for all recordings (using JMP Pro 13; SAS Institute Inc., Cary, NC). From the PCA analysis, we obtained 3 principal components (PCs), which explained 98% of the total variation in the calls. Note that the previously recorded calls were only used in PCA analysis; all other analyses reported here include only the calls recorded in 2016 and 2017 because those were the calls for which we had measures of total *Spea* and nearest neighbor distances.

We next used normal mixture clustering with the PCs and compared Akaike information criterion corrected for small sample sizes (AICc) values to determine the most likely number of clusters in sound space. We chose the model with the lowest AICc value by a minimum of 4 AICc units. Based on our genotyped samples, these clusters closely reflected a combination of call type (fast or slow) and species (*S. bombifrons*, *S. multiplicata*, or hybrid.) The 3 known hybrids from our 2016 and 2017 data set and all ungenotyped individuals that clustered with the known hybrids in our PCA ( $N = 2$ ) were eliminated from further analysis. This procedure left us with the following sample sizes across 43 populations: 108 *S. multiplicata*, 206 slow *S. bombifrons*, and 39 fast *S. bombifrons*. Note that this PCA approach was used strictly to identify possible hybrids that could impact our results when we analyzed each call parameter separately as described below.

### Statistics

In separate analyses for each male type and call parameter (pulse rate, call rate, dominant frequency, and call duration), we used stepwise model comparison to measure the effects of distance to the nearest neighbor and total calling *Spea* on a given call parameter. Beginning with a complete model including the male’s population as a random effect and all covariates (see below), we eliminated nonsignificant variables based on the results of an analysis of variance (employing the “Anova” function in the “car” package in R 3.4.1). Because temperature can impact call rate, pulse rate, and call duration (Gerhardt and Huber 2002), we included water temperature as a covariate in all models for those call parameters. Similarly, dominant frequency is influenced by body size and shows a latitudinal cline (in addition to changes in body size), so we included body size and latitude as covariates in our model of dominant frequency (Zweifel 1968). One breeding aggregation in which we recorded both *S. multiplicata* and slow-call *S. bombifrons* had an extremely high number of *Spea* relative to all other aggregations. Although this population was an outlier, it nevertheless represents real biological variation and a population in which competitively mediated effects could be important. We therefore included it in our analyses. However, for those models where inclusion of this population impacted the results, we report our findings with and without this population included.

## RESULTS

For males of all 3 call types, varying numbers of total calling *Spea* in the breeding aggregation and/or varying distance to their nearest neighbor corresponded to changes in call parameters (Table 1). However, the 3 groups differed in the specific call parameters that showed significant associations with these measures of reproductive interference from competing males (Table 1).

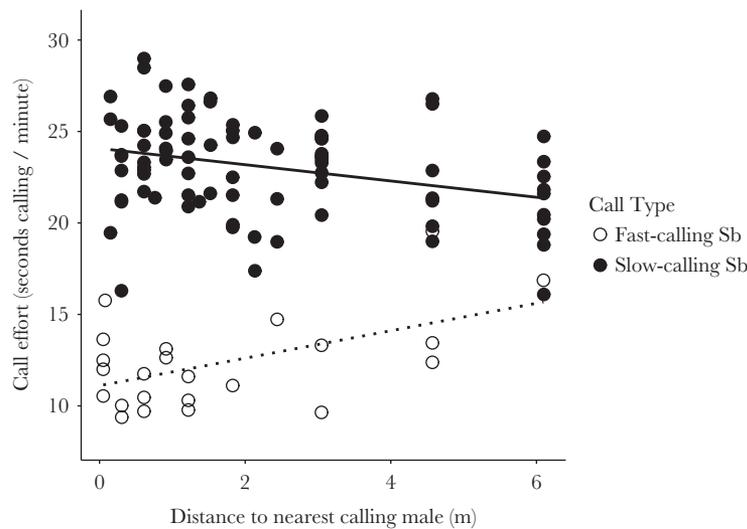
We found that in *S. multiplicata* calls, pulse rate and call rate decreased, whereas call duration increased in response to increasing

**Table 1**  
**Effects of main predictor variables on call characters for *S. multiplicata* (Sm), and fast- and slow-calling *S. bombifrons* (Sb)**

Predictor variable	Species, call type	Pulse rate	Call rate	Duration	Dominant frequency	Calling effort
Total calling <i>Spea</i>	Sm	$\chi^2 = 4.79$ $P = 0.018$ $\beta = -0.02$	$\chi^2 = 9.94$ $P = 0.002^*$ $\beta = -0.04$	$\chi^2 = 7.28$ $P = 0.007^*$ $\beta = 0.002$	$\chi^2 = 1.13$ $P = 0.29$	$\chi^2 = 0.72$ $P = 0.40$
	Sb, slow	$\chi^2 = 6.79$ $P = 0.009$ $\beta = -0.03$	$\chi^2 = 0.11$ $P = 0.73$	$\chi^2 = 0.28$ $P = 0.59$	$\chi^2 = 0.13$ $P = 0.72$	$\chi^2 = 0.11$ $P = 0.74$
	Sb, fast	$\chi^2 = 0.52$ $P = 0.47$	$\chi^2 = 0.23$ $P = 0.63$	$\chi^2 = 0.89$ $P = 0.34$	$\chi^2 = 3.19$ $P = 0.07$ $\beta = -1.23$	$\chi^2 = 0.96$ $P = 0.33$
Nearest neighbor distance	Sm	$\chi^2 = 2.00$ $P = 0.16$	$\chi^2 = 8.01$ $P = 0.005$ $\beta = 0.78$	$\chi^2 = 5.72$ $P = 0.017$ $\beta = -0.04$	$\chi^2 = 2.81$ $P = 0.09$ $\beta = 20.71$	$\chi^2 = 0.32$ $P = 0.57$
	Sb, slow	$\chi^2 = 0.82$ $P = 0.37$	$\chi^2 = 0.97$ $P = 0.32$	$\chi^2 = 3.20$ $P = 0.07$ $\beta = -0.01$	$\chi^2 = 0.81$ $P = 0.37$	$\chi^2 = 5.20$ $P = 0.023$ $\beta = -0.37$
	Sb, fast	$\chi^2 = 0.07$ $P = 0.78$	$\chi^2 = 20.21$ $P < 0.001$ $\beta = 5.31$	$\chi^2 = 0.28$ $P = 0.60$	$\chi^2 = 1.75$ $P = 0.19$	$\chi^2 = 8.80$ $P = 0.003$ $\beta = 0.77$

Degrees of freedom = 1 for all contrasts. See Methods and Results for details.

\*Indicates results that are sensitive to the large outlier population; all become not significant at  $P < 0.05$  with outlier removed.



**Figure 2**

Fast- and slow-calling *S. bombifrons* showed opposite patterns of call effort with increasing distance from the nearest neighboring male.

numbers of total calling *Spea* (Table 1). However, this effect of total *Spea* was sensitive to the presence of an unusually large aggregation in our data. When this aggregation was removed from the analysis, the effect of total *Spea* on call rate was marginally not significant ( $\chi^2 = 3.51$ , degrees of freedom [df] = 1,  $P = 0.06$ ), and the effect of total *Spea* on call duration was not significant ( $\chi^2 = 0.63$ , df = 1,  $P = 0.43$ ). Whether these 2 *S. multiplicata* call parameters vary in association with total calling *Spea* is, therefore, unclear. Regardless of whether *S. multiplicata* calls vary in response to total *Spea*, we found no effect of total *Spea* on male calling effort. We also found no effect of total *Spea* on dominant frequency (Table 1).

We further evaluated whether attributes of *S. multiplicata* calls varied with distance between nearest neighbors. We found that pulse rate and dominant frequency did not vary with nearest neighbor distance (Table 1). However, *S. multiplicata* calls increased

in duration and decreased in call rate as nearest neighbor distance decreased (Table 1). Despite this association, we found no relationship between nearest neighbor distance and *S. multiplicata* males' calling effort.

For the slow-calling *S. bombifrons*, we found that call pulse rate declined with increasing numbers of total calling *Spea*. We found no other associations between call rate, call duration, or call dominant frequency and either total calling *Spea* or nearest neighbor distance (Table 1). Despite finding no significant effect of nearest neighbor distance on call rate or duration, we found that call effort in slow-calling *S. bombifrons* was negatively associated with the distance to the nearest neighbor. As the distance decreased, male call effort increased (Table 1; Figure 2).

In contrast to slow-calling *S. bombifrons* (and possibly *S. multiplicata*), fast-calling *S. bombifrons* did not show any associations

between any aspect of their calls and total calling *Spea* (Table 1). However, fast-calling *S. bombifrons* calls did vary as a function of the distance to their nearest neighbor. Males had slower call rates and lower call effort the closer they were to neighboring males (Table 1; Figure 2).

## DISCUSSION

As in other species (e.g., Greenfield 1994; Grafe 1996, 2003; Greenfield 2005; Martinez-Rivera and Gerhardt 2008), *S. multiplicata* and *S. bombifrons* males showed competitively mediated changes in their signals depending on the nature of the noisy, competitive environment in which they were signaling (characterized here by total calling *Spea* and nearest neighbor distance). Moreover, the 2 species—and the 2 different types of *S. bombifrons*—differed in the call parameters that varied across signaling environments. Our results suggest that different types of males vary in their responses to noisy, competitive environments, and that this variation can be explained, at least in part, by particular aspects of the males' signal structure.

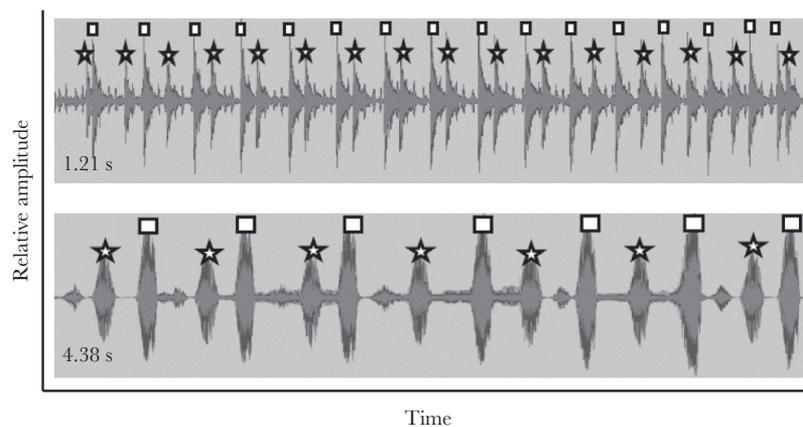
Generally, selection should shape male signals to enhance their detection in their environment (Wiley 1994; Bradbury and Vehrencamp 1998; Brumm and Slabbekoorn 2005; Greenfield 2005). For this reason, the nature of male signals might be expected to impact how those signals change in response to a noisy, competitive environment. Evaluating this possibility is important because such changes have implications for male investment in signaling and sexual selection (Greenfield 1994).

In spadefoots, *S. multiplicata* and slow-calling *S. bombifrons* have similar call structure with relatively long calls and clearly discrete pulses (Figure 1). As might be expected from their similar call structure, we found that both types showed similar responses to their environment. One response that both groups showed was a pattern of decreasing pulse rate as the total number of *Spea* in a breeding aggregation increased. A possible explanation for this pattern is that slower pulse rates enable *S. multiplicata* and slow-calling *S. bombifrons* males to interdigitate their pulses with competitors and thereby reduce signal overlap (Grafe 2003; Martinez-Rivera and Gerhardt 2008). Although we observe males of these species alternating calls, suggesting that males do not interdigitate pulses in all circumstances, almost all recordings of multiple males in close proximity involve some degree of call overlap, and in these periods of overlap

pulses are often interdigitated (Stirman R, Pfennig KS, personal observations; Figure 3).

In addition to changes in pulse rate, *S. multiplicata* showed increased call duration as nearest neighbor distance decreased (Table 1). Changes in call duration can reflect trade-offs between call rate and call duration such that faster calling usually results in shorter calls and vice versa (Wells and Taigen 1986). Additionally, increased call duration might reduce the potential for the males' calls to be entirely overlapped by a neighbor (Schwartz et al. 2008) and could thereby enhance detectability of a male's signal by females (Greenfield 1994; Greenfield 2005). A third possibility, particularly for *S. multiplicata*, which showed simultaneous changes in pulse rate and duration, is that the increased duration is the result of males increasing the space between pulses to interdigitate them. Regardless, our findings are consistent with those in other anurans, where modifying pulse rate and call duration are common responses to a noisy, competitive signaling environment, especially in species with spaced pulses (Wells and Taigen 1986; Wagner 1989; Martinez-Rivera and Gerhardt 2008).

In contrast to *S. multiplicata* and slow-calling *S. bombifrons*, fast-calling *S. bombifrons* showed no associations between any call parameter and the total number of *Spea* and no effect of nearest neighbor distance on pulse rate or call duration (Table 1). Instead, fast-calling *S. bombifrons* showed a pattern of reduced call rate and calling effort as nearest neighbor distance declined. These differences between fast- and slow-calling male call types might be due to differences in call structure. Fast-calling *S. bombifrons* produce extremely short calls with indistinct pulses (Figure 1). Because there is no space between pulses, fast-calling *S. bombifrons* males cannot interdigitate their calls without entirely changing the nature of their calls (Figure 1). Instead, changes in call rate might enable males to better alternate calls with neighboring males so as to minimize the potential for interference with competitors (Figure 3; e.g., Schwartz 1987). Indeed, fast-calling *S. bombifrons* are frequently observed alternating calls with one another without call overlap (Stirman R, Pfennig KS, personal observations; Figure 3). Still, it was surprising that fast-calling *S. bombifrons* reduced call rate and call effort in response to competition. This is because in many anurans, females prefer faster call rates and/or higher calling efforts, both of which can indicate that males are in better condition (Pfennig 2000; Gerhardt and Huber 2002; Pfennig 2008). Thus, males calling close together might be expected to increase—not decrease—their call rate or call effort to outcompete their neighbors.



**Figure 3.**

Alternative strategies to avoid call overlap between different call structures. Top panel: a field recording of 2 *S. multiplicata* calling simultaneously with interdigitated pulses. Bottom panel: field recording of 2 fast-call *S. bombifrons* alternating their calls. Different symbols = different individuals.

That fast-calling *S. bombifrons* show the opposite of the expected pattern in call rate and effort might indicate a selective trade-off. If females strongly discriminate against overlapped calls, then slower call rates and lower call efforts might be favored in noisy environments even though slower call rates or lower call efforts might be unattractive to females in the absence of competitors' signals. Males might compensate for the decrease in call rate or call effort by altering their calls once a female approaches in close proximity (Reichert 2013). Specifically, fast-calling *S. bombifrons* males might attract females from a distance with unobscured calls but then increase their call rates without regard to call overlap when a female approaches. Consistent with this possibility, fast-calling *S. bombifrons* males facultatively increase their call rates in response to the approach of a female (Stirman R, and Pfennig KS, personal observations). Overall, this suggests that the distribution of male signals in a given aggregation might depend not only on interactions among males but also the frequency of interactions with females (Greenfield 1994).

Although our comparison is limited to 3 groups, the differences in response to reproductive interference between *Spea* with slower calls (*S. multiplicata* and slow-calling *S. bombifrons*) and *Spea* with faster calls (fast-calling *S. bombifrons*) are consistent with the hypothesis that signal structure impacts how male sexual signals change (either facultatively or evolutionarily) in response to competition with other males. For *Spea* males with slower call types, changes in pulse rate and call duration might be the most effective response to noisy, competitive environments, whereas changes in call rate might be the most effective response for the fast-calling males. Generally, male signals are expected to evolve and/or be facultatively modified in a way that enhances male success in competitive interactions with other males and mate attraction (Greenfield 1994; Wiley 1994; Bradbury and Vehrencamp 1998; Brumm and Slabbekoorn 2005; Greenfield 2005). Our results suggest that the nature of the signal itself could play an important role in how that signal is further modified in response to variation in the competitive environment.

Another important result that emerged from our study was that the male types differed in how their call effort (total time spent calling per minute) was impacted by signal interference (Table 1). Although signal interference from competitors might be expected to increase male calling effort (Zahavi and Zahavi 1999), we did not find this prediction supported across all male groups. Instead, we found that whereas slow-calling *S. bombifrons* increase calling effort as neighbors get closer, fast-calling *S. bombifrons* reduce calling effort as neighbors get closer (Figure 2). In *S. multiplicata*, nearest neighbor distance had no effect on male calling effort (Table 1). These differences suggest that the energetic costs of signaling in noisy, competitive environments can differ for males of different call types. This variation in the consequences of competition could drive variation in male investment in sexual signaling and patterns of sexual selection across species. More work is needed to understand how species-specific variation in the costs of competition impact diversity in reproductive investment and sexual signals across species.

In sum, our results suggest that noisy, competitive environments can drive changes to signals that depend on signal structure. How such variation in turn generates diversity among species in patterns of energy investment, mate choice, and sexual selection remain open issues that could provide further insight into competition's role in signal diversity.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Stirman and Pfennig (2019).

**Handling editor:** Jonathan Pruitt

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