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Multiple signals and male spacing affect female preference at cocktail parties in treefrogs

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Effective acoustic communication in the face of intense conspecific background noise constitutes a constant sensory challenge in chorusing and colonial species. An evolutionary approach suggests that behavioural and environmental constraints in these species should have shaped signal design and signalling behaviour to enable communication in noisy conditions. This could be attained both through the use of multicomponent signals and through short-term adjustments in the spatial separation of calling males. We investigated these two hypotheses in a chorusing anuran, the hylid *Hyla arborea*, through a series of phonotaxis experiments conducted within a six-speaker arena in a high background noise situation, by presenting females with male calls containing either single or multiple attractive call components, and by modifying distances between speakers. We found that female ability to discriminate attractive calls increased when several attractive call components were available, providing novel evidence that the use of multicomponent signals enhances communication in complex acoustic conditions. Signal discrimination in females also improved with speaker separation, demonstrating that within natural choruses, spatial unmasking conditioned by male density and spatial separation probably improves female discrimination of competing males. Implications of these results for the accuracy of mate choice within choruses are discussed.

Keywords: sexual selection; background noise; multiple signals; mate choice; anurans

1. INTRODUCTION

One inescapable feature of our natural world is its constant noise. Whatever its source, ubiquitous environmental noise has long been established as a major impediment to effective acoustic communication. Thus regarding climatic noise, Lengagne *et al.* (1999*a*) demonstrated that wind makes call discrimination more difficult in penguins (*Aptenodytes patagonicus*), and Lengagne & Slater (2002) found a 69-fold decrease in the area reached by the calls of male tawny owls (*Strix aluco*) in rainy versus dry conditions. Concerning biotic noise, conspecific colonies and choruses generate particularly constraining communication conditions: dozens of closely packed sound sources simultaneously produce competing calls presenting a high degree of spectral and temporal overlap (Lengagne *et al.* 2001; Bee & Micheyl 2008). Such a noisy environment can have detrimental effects on the fitness of both the sender and the intended receiver of information, when it impairs communication. This is typically the case for intersexual communication, in which females rely on male calls to discriminate male quality and thus gain direct or indirect benefits through their choice of mate (Andersson 1994). An evolutionary approach thus suggests that the behavioural and environmental constraints of species regularly exposed to social noise should have shaped their acoustic signal design and auditory system as well as signalling behaviour to enable signal perception in noisy conditions.

The issue of communication in noisy social settings in humans has been the focus of much research since the problem—aptly named the cocktail party problem—was first raised by Cherry (1953). Surprisingly however, little is known of the sensory solutions to the cocktail party problem existing in non human animals (reviewed in Bee & Micheyl 2008). Interestingly, in a recent review on communication, Candolin (2003) brought to light the long-overlooked necessity of considering signals not as single but as multi-dimensional entities and suggested that complex signals could constitute a solution to communication in noisy environments. Hebets & Papaj (2005) further developed this theory through their 'efficacy backup hypothesis' which predicts that the use of complex signals containing multiple components with differing transmission properties should enable a message to be transmitted in a variety of environmental conditions. Although the existence of multiple sexual signals has often been found in studies of sexual selection in chorusing species (reviewed in Gerhardt & Huber 2002), no study has to date investigated whether their use enables accurate mate choice in the naturally noisy environment of these species.

Chorusing anurans constitute an ideal candidate for the use of multi-component acoustic sexual signals. Among nocturnal chorusing anurans, the hylid *Hyla arborea*, in which sexual selection has been observed to take place through female mate choice (Friedl & Klump 2005; Richardson *et al.* 2008, submitted), is exceptional in presenting the highest calling metabolism measured

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so far in ectothermic vertebrates (Grafe & Thein 2001), signifying that the males invest enormous amounts of energy in their acoustic sexual displays. The male advertisement call has been extensively described (Friedl & Klump 2002) and two-choice phonotaxis experiments we conducted on females in quiet conditions (Richardson *et al*. submitted) have shown that females use several temporal, spectral and amplitude parameters of this call in their choice of mate.

The first objective of this study was therefore to investigate whether the simultaneous use of these multiple call components does effectively enhance female discrimination of male quality in chorus conditions. In order to do this we conducted female phonotaxis tests in a high background noise situation within a six-speaker arena, and compared female ability to discriminate attractive calls based on either a single attractive call component or on a combination of attractive call components. In addition to evolutionary or ontogenetic shaping of signal design, a few studies conducted on chorusing anurans have found that short-term adjustments in the spatial separation of calling males improve female discrimination of male calls in treefrogs (Schwartz & Gerhardt 1989; Bee 2008). Our second objective was therefore, by modifying the distances between speakers within the experimental arena, to determine whether male spacing further affects female discrimination of multiple calls in chorus conditions.

2. MATERIAL AND METHODS

(a) *Study site and collection methods*

During the breeding period, from April to May, we collected female European treefrogs from a large metapopulation situated in the Ile Cremieu area, southeast France (45°45′10″ N, 5°19′56″ E). Females found in the water or around the two prospected ponds were collected, placed in individual boxes, and brought back to the laboratory for testing in the hours to follow.

(b) *Arena design and playback systems*

In order to meet the challenge of studying mate choice in realistic acoustic conditions, we designed an experimental arena in which we could reproduce two major acoustic constraints inherent to natural choruses: multiple sound sources and constant background chorus noise. For details concerning electronic equipment, please refer to the electronic supplementary material 1.

We conducted three series of experiments. In experiments 1 and 2, females were tested in a hexagonal arena of 0.4 × 2.0 m (height × diameter). The floor was covered with low-pile carpet and the inside of the walls and ceiling were lined with 60 mm-thick anechoic foam wedges (Plastiform) to limit sound reverberation. To shield the observers from detection by the females, 1 m high frames supporting a light black cloth were set up around the arena. Dim red light was provided by a red bulb hung 1 m above the centre of the arena. In order to reproduce chorus conditions, six loudspeakers were positioned around the chamber, one in each angle of the arena. Neighbouring speakers were thus separated by a 60° angle, and opposing speakers were 2 m apart.

At the onset of each test the six acoustic stimuli were randomly attributed to the six speakers and broadcast antiphonally throughout the test with a 1.5 s interval of silence between successive stimuli, meaning there were effectively no leading or following calls. This enabled us to prevent female choice from being influenced by the female preference for leading calls which has been shown to exist in this species through 2-stimuli choice tests (Richardson *et al*. 2008). The amplitudes of these test call bouts were set at the realistic value of 84 dB at the release point in the centre of the arena.

One metre above the female release point in the centre of the arena a recording of a conspecific chorus (a 16 s selection of a recording of chorus noise (approx. 15 males) made on the study site in 2005, which lacked any distinct *H. arborea* calls and presented a nearly constant amplitude) was broadcast continually from a CD player. This enabled us to ensure that acoustic masking by chorus noise would be the same for all acoustic stimuli at the female release point. Because treefrogs inhabit and breed in three-dimensional environments, females regularly encounter noise, and mating calls, coming from above. Chorus noise amplitude was set at 78 ± 1.5 dB at the female release point, i.e. 6 dB below test call bout broadcast amplitude, following the same procedure as for the test call bouts. This corresponded to a level of conspecific background noise regularly measured throughout the breeding period at the breeding site of the study population (C. Richardson 2009, unpublished data).

Experiment 3 was conducted in an arena identical in all points to the one described above, save that the distance between opposing speakers was doubled to 4 m.

(c) *Preparation of the acoustic stimuli and female preference tests*

In a previous study (Richardson *et al*. submitted) conducted on mate choice in *H. arborea* in simple acoustic conditions (two-stimuli choice tests, no background noise) we found a significant female preference for calls with (i) a high amplitude, (ii) a low peak frequency (i.e. the frequency with the highest energy content), and (iii) a short call duration linked to a high call rate. The aim of the present study was to investigate female ability to discriminate these three cues in more realistic acoustic conditions. In order to do this, we used Avisoft SAS-lab Pro software (Avisoft Bioacoustics) to synthesize 16-bit audio files with a 16 kHz sampling rate containing the acoustic stimuli (for details on the characterisation of the male advertisement call and the construction of synthetic calls please refer to the electronic supplementary material 2). These were an 'average synthetic call bout', referred to as the 'control bout', (with mean population values for all acoustic characteristics save bout length which we set at 12 calls per bout, see the electronic supplementary material 2, table S1) and four test call bouts which varied independently in the following characteristics found to be involved in mate choice (Richardson *et al*. submitted): peak call frequency, call amplitude, call duration and call rate (test bouts 1–4 in the electronic supplementary material 2, table S1). Prior to this study we had verified in two-choice phonotaxis tests that females do not discriminate between natural call bouts with mean population values for all acoustic characteristics and the synthetic average call bouts (chi-square test: $n = 18$, $\chi^2 = 0.2222$, d.f. = 1, p-value = 0.637).

Using these synthetic call bouts we conducted the following three series of phonotaxis experiments (all were conducted in the presence of conspecific chorus noise broadcast from the overhead speaker):

(i) *Experiment 1: can females discriminate male calls in a realistic acoustic context on the basis of a single call component?*
Experiment 1a: female discrimination of peak frequency in chorus conditions (*control bout* versus *test bout 1 of the electronic supplementary material 2, table S1*):

We first presented females with a choice between five speakers broadcasting the 'control bout' and one speaker emitting test bouts identical for all call parameters save peak frequency which was 1 s.d. below the population mean (197 Hz).

Experiment 1b: female discrimination of call amplitude in chorus conditions (*control bout* versus *test bout 2 of the electronic supplementary material 2, table S1*):

We gave females a choice between five 'control bout' speakers and one speaker for which call amplitude was increased 2 s.d., i.e. 6 dB, above the population mean.

Experiment 1c: female discrimination of call rate and duration in chorus conditions (*test bout 3* versus *test bout 4 of the electronic supplementary material 2, table S1*):

Because call rate and duration are negatively correlated in *H. arborea* (Friedl & Klump 2002), we took this correlation into account when investigating female use of temporal call components. We thus presented females with a choice between call bouts with equivalent total calling time and bout length, but differing in call rate and duration values. Five speakers broadcast call bouts with long call durations (mean + 2 s.d.: 70 ms) and a low call rate (6.4 calls per second) while one speaker emitted calls of short call duration (mean − 2 s.d.: 40 ms) with a high call rate (11.2 calls per second).

(ii) *Experiment 2: can females discriminate male calls in a realistic acoustic context on the basis of multiple call components?* (*test bout 5* versus *test bout 6 of the electronic supplementary material 2, table S1*)

We gave females a choice between five speakers broadcasting test bouts with mean population values for all parameters save call duration which was 2 s.d. above the population mean (associated with a low call rate), and one speaker emitting calls with peak frequency 1 s.d. below, amplitude 2 s.d. above, and duration 2 s.d. below (associated with a high call rate) the population mean.

(iii) *Experiment 3: does male spacing affect female discrimination of multicomponent calls in a realistic acoustic context?* (*test bout 5* versus *test bout 6 of the electronic supplementary material 2, table S1*)

We repeated experiment 2 within an arena in which opposing speakers were separated by 4 m, mimicking less constrained male spacing.

(d) *Experimental procedure*

The tests took place between the hours of 22.00 and 06.00. At the beginning of each trial a female was placed in a circular, acoustically transparent (plastic mesh) cage (70 × 50 mm, diameter × height) located in the centre of the arena. After the alternative stimuli had been broadcast antiphonally for 2 min, the top of the cage was lifted remotely by pulling a string, and the female's movements were monitored. A choice was scored when the female positioned herself on the membrane of one of the speakers or within 10 cm of it and remained there for at least 60 s. If no choice was made within 20 min or if the female exited the testing area, the trial was discarded and the female was retested later in the night. Between each trial the six test call bouts were randomly reattributed to the six loudspeakers to avoid possible side biases.

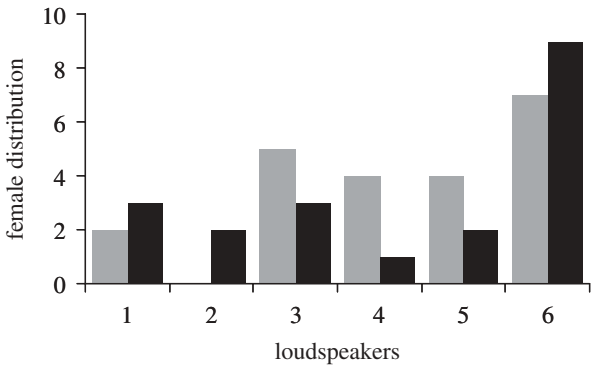

Figure 1. Female distribution in experiments 2 (grey bars) and 3 (black bars) between loudspeakers 1 and 5, broadcasting control bouts, and loudspeaker six broadcasting call bouts presenting attractive values of call amplitude, peak frequency and temporal call components. Female preference for the latter was marginally significant in experiment 2 (two-tailed binomial test: $n = 22$, $p = 0.061$) and significant in experiment 3, in which between-speaker distance was doubled (two-tailed binomial test: $n = 20$, $p = 0.003$).

Because of the scarcity of females available during one breeding season, each female was used in four tests, but we never tested a given female more than once within a given experiment. Test sequence was randomized for each female to control for any order effect. After testing, all the females were released the following night at their site of capture. For further details concerning female utilization please refer to the electronic supplementary material 3.

Female preference was investigated using two-tailed binomial tests with R v 2.7.0 statistical analysis software (R Development Core Team 2008). We tested the null hypothesis that the probability of the females' successfully identifying the loudspeaker emitting the most attractive calls was 1/6. Results are presented in the form mean ± s.d.

3. RESULTS

Concerning female preference, in experiment 1, females did not discriminate calls in a chorus context on the basis of a single call component, be it peak frequency (experiment 1a, $n = 19$, $p = 0.199$), call amplitude (experiment 1b, $n = 18$, $p = 0.827$) or call rate and call duration (experiment 1c, $n = 20$, $p = 0.335$). However, call discrimination improved when call attractiveness was determined simultaneously by three call components, with a marginally significant proportion of females correctly choosing the loudspeaker broadcasting the more attractive calls (experiment 2, $n = 22$, $p = 0.061$, see figure 1). When inter-male distances doubled while male angular separation remained constant, female preference for the loudspeakers emitting calls presenting multiple attractive cues became highly significant (experiment 3, $n = 20$, $p = 0.003$, see figure 1).

Concerning female behaviour in the arena, females tended to spend on average close to twice as long assessing male quality when call attractiveness was determined simultaneously by three call components (choice duration was, respectively, 308.5 ± 318.6 s and 383.1 ± 331.7 s for experiments 2 and 3) as when it

was based on a single call component (choice duration was, respectively, 167.9 ± 174.2 s, 162.4 ± 136.9 s and 217.7 ± 181.8 s for experiments 1a, 1b and 1c).

4. DISCUSSION

(a) *Female discrimination based on single call components in realistic acoustic conditions (experiment 1)*

Unlike in two-stimuli phonotaxis tests conducted in quiet conditions (Richardson *et al.* submitted), females were unable to identify calls presenting either a higher amplitude, a faster call rate or a lower fundamental frequency in multi-speaker, high background noise choice tests. While several studies have considered the effect of chorus conditions on mate choice, to our knowledge this constitutes the first study in which acoustic complexity was generated by simultaneously incorporating masking background noise (with a signal-to-noise ratio of +6 dB), multiple callers (six signal speakers) and variable spatial gaps between sequentially calling males which characterize natural choruses.

Several factors probably contribute to this breakdown in female discrimination. One of these is background noise which has been shown in previous studies (Gerhardt & Klump 1988; Wollerman 1999; Wollerman & Wiley 2002) to effectively mask individual male calls at signal-to-noise ratios commonly measured within treefrog choruses (+9 dB and lower).

In addition to background noise, the multiplication of the number of competing sound sources in choruses has been shown to affect signal discrimination in several species (e.g. Marquez & Bosch 1997). In this study the competing calls presented no time overlap, suggesting that energetic masking is not involved. Rather, signal detection theory predicts that increasing the number of possible signals increases the uncertainty that any one signal will occur and thus reduces its discriminability, a result confirmed for human subjects (Swensson & Judy 1981).

Finally, in the present study, at the onset of each test we randomly set the order in which the six loudspeakers successively broadcasted the test call bouts. Speakers broadcasting calls consecutively thus presented variable spatial gaps between each other. Although the sequence in which the stimuli were broadcast was not modified during a given test, we were thus able to simulate to a certain extent the variability of the spatial gaps which exist between sequentially calling males in natural choruses. Bosch & Boyero (2006) showed in eight-speaker tests that when call emission was not regular (variable spatial gaps between speakers emitting consecutive stimuli), female ability to choose the most attractive loudspeaker was affected. These results suggest that the unpredictability of the spatial disposition of sequentially calling males could also affect female ability to locate the most attractive calls within choruses.

(b) *Multicomponent signals and communication effectiveness*

Clearly, conspecific noise generates constraining conditions for effective communication (Lengagne *et al.* 1999*b*). This is amplified by the constant spatial and temporal variation in masking noise which exists within colonies and choruses, due to such factors as the number of callers, their relative positions, their degree of call overlap and the structure of the surrounding habitat. However, just as is the case for certain habitats characterized by particular abiotic noise (e.g. Feng *et al.* 2006), the acoustic constraints inherent to conspecific choruses may act as a selective pressure upon the evolution of acoustic signalling, shaping acoustic signal design as well as the auditory system to enable efficient communication (Lengagne *et al.* 2001). Candolin (2003) and Hebets & Papaj (2005) suggest that signal masking by unpredictable background noise may have driven the evolution of multicomponent acoustic signals: the use of signals containing several informative components with differing transmission properties could allow a message to be transmitted and received successfully in varying conditions of environmental noise.

To date, surprisingly, very little work has investigated the import of multiple signals for communication in complex conditions. Concerning variation in environmental light and substrate, Hebets *et al.* (1996) and Hebets & Uetz (1999) found that the wolf spider *Schizocoza retrorsa*, a species with both visual and vibratory courtship signals, can procure just as many copulations in varying light (dark versus light) and substrate (granite versus filter paper) conditions. Concerning social environmental noise however, no study has to our knowledge, tested this hypothesis directly. Although students of sexual selection in chorusing anurans and insects have been aware for decades that females use several call components for mate choice, all the work conducted to date on mate choice in chorus conditions (masking chorus noise or multiple sound sources) has focused on female discrimination of single male call components (Gerhardt & Klump 1988; Wollerman 1999; Wollerman & Wiley 2002). The present study found that female ability to discriminate and localize the more attractive calls in complex acoustic conditions increases when many call components are available (experiments 1 and 2). To our knowledge this result constitutes the first piece of evidence supporting the much cited theory that the use of multicomponent signals enhances intersexual communication in complex acoustic conditions.

(c) *Male spatial separation and communication effectiveness within choruses*

In addition to evolutionary or ontogenetic shaping of signal design, various short-term adjustments by animals in their calling behaviour in response to changing noise conditions can also enhance communication effectiveness. One such adjustment is the spatial separation of calling males, which has been shown in many species to be highly variable (including in *H. arborea*: C. Richardson 2009, personal observation) and mediated by acoustic cues (e.g. Murphy & Floyd 2005). In the present study (experiments 2 and 3) we found that female ability to discriminate multicomponent acoustic signals was greatly enhanced when both the distance between neighbouring speakers and the distance between speakers and the overhead source of background noise were doubled. It is noteworthy that the signal-to-noise ratio at the female's release point was maintained identical for both distances tested, so that at the female's release point the only

element changing between experiments 2 and 3 was the spatial separation of competing sound sources. The effect of male spatial disposition on acoustic signal perception by females, known as spatial unmasking, has been studied recently in treefrogs (Schwartz & Gerhardt 1989; Bee 2008). As predicted by the spatial unmasking theory, female *H. cinerea* discrimination was found to increase with the angular separation of signal speakers and noise sources (Schwartz & Gerhardt 1989).

In all these studies of spatial unmasking the authors suggest that their experimental setup simulates a situation that females would encounter on entering a chorus from the periphery, in which case they would perceive individual calling males and general background chorus noise as originating from different locations. In contrast with that approach, in the present study we chose to investigate the effect of the spatial separation of multiple individual callers within a general high background noise setting (with chorus noise broadcast from above the female release point). By increasing the distance between speakers while maintaining a constant angular separation between the speakers in a high background noise situation, we thus reproduced a situation which females face when sampling males within a chorus. The finding that in our study female ability to discriminate male calls increased with speaker separation thus provides the novel result that within natural choruses, spatial unmasking conditioned by male density and male spatial separation—independently of the level of masking background noise which was maintained constant in our study probably improves female discrimination of competing male calls.

(d) *Conclusion*

This study has brought to light that although the complex acoustic conditions inherent to natural choruses do impose constraints on intersexual communication, the use of multicomponent acoustic signals constitutes a key to overcoming the cocktail party problem in chorusing anurans. Communication efficiency was found to be conditional to male spatial separation. Thus, the selection gradient on male calls is predicted to be affected by chorus density. However, several authors (e.g. Candolin 2003) have suggested that the use of an additional sensory channel may allow chorusing species to compensate for the masking of their vocalizations, by conveying multiple messages or facilitating the transfer of acoustic information by increasing the probability of call detection. In accord with this prediction we recently found that female *H. arborea* base their choice of mate not only on male vocalizations, but also on visual male signals (Gomez *et al.* 2009) which we found to be carotenoid-based (Richardson *et al.* 2009). Further studies are now necessary to determine whether the use of such multimodal signals can constitute a solution to effective communication in acoustically constraining dense chorus situations.

This study was conducted in accordance with the current laws in France and with the approval of the Préfecture de l'Isère (decision 2007-03 328) as well as that of the Direction of Veterinary Services (DSV n°69266347).

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