



Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog

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Many animals communicate in environments with high levels of background noise. Although it is a fundamental prediction of signal detection theory that noise should reduce both detection and discrimination of signals, little is known about these effects in animal communication. Female treefrogs, *Hyla ebraccata*, in Costa Rica choose mates in large noisy multispecies choruses. We tested gravid females for preferences between computer-synthesized calls with carrier frequencies of 3240 and 2960 Hz (values near the mode and the fifth percentile of the population, respectively) in four levels of background noise from a natural chorus. In the absence of noise (signal/noise ratio >25 dB), females preferred the lower frequency. With moderate signal/noise ratios (6 and 9 dB), they did not discriminate between these frequencies. With low signal/noise ratios (3 dB), females preferred the frequency near the mode for the population. Similar experiments had previously demonstrated that females can detect the presence of a male's calls with signal/noise ratios of 3 dB or greater. Thus moderate levels of natural background sound reduced a female's ability to discriminate between males' calls even when she could detect them. In high levels of background sound, females abandoned discrimination for low-frequency calls and reverted to the task of detecting signals with modal properties for the population. These results justify recent theoretical analyses of the importance of receivers' errors in the evolution of communication.

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Until recently few discussions of the evolution of communication have considered the consequences of errors by individuals responding to signals. Although it is clear that such errors would reduce the expected benefits of responding, it has not been so clear that these changes in benefits could have fundamental consequences for the evolution of communication. Recent theory, however, has emphasized the importance of errors both in applications of game theory to interactions between signallers and receivers (Johnstone 1994, 1997, 1998, 1998; Johnstone & Earn 1999) and in applications of signal detection and decision theory to optimization of receivers' behaviour (Wiley 1994, 2000). This study tests a prediction of signal detection theory that has basic consequences for understanding the evolution of communication: when errors are likely, discrimination between two kinds of signals is a more difficult task than detection of one kind of signal.

Many animals communicate in situations that make errors likely, either because high levels of background

energy mask relevant signals or because relevant and irrelevant signals differ only slightly. Mating aggregations of frogs provide particularly clear cases. Individual males produce advertisement calls for attracting mates in an environment with nearly continual background sound from other males of the same and often other species.

Females' responses to males' calls can often be studied in a laboratory by giving females a choice between two loudspeakers. By consistently approaching one loudspeaker, female frogs have shown preferences not only for conspecific over heterospecific males' calls but also among conspecific calls that differ in such features as pulse rate or dominant frequency (reviewed by Gerhardt 1994, 1995; Wells 1977). In this context, 'choice' indicates a subject's behaviour in one test and 'preference' a trend demonstrated by many choices.

Although most such studies have used quiet rooms with low levels of background sound, there is clear evidence that the background sounds from a chorus can alter the subjects' behaviour. Overlapping calls of nearby males affect both the behaviour of calling males and the preferences of gravid females (reviewed by Wells and Schwartz 1984; Narins & Zelick 1988; Wells 1988; Greenfield 1994). In addition, continuous broadband noise affects the ability of females to detect males' calls

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(Ehret & Gerhardt 1980; Bailey & Morris 1986; Gerhardt & Klump 1988; Brush & Narins 1989; Schwartz & Gerhardt 1989; Klump 1996; Wollerman 1999).

The effect of background sound is particularly striking on females' ability to detect any one individual male's calls. Because of the difficulties of detection, a female can detect only one or a few individual males from any one spot in a chorus (Gerhardt & Klump 1988; Wollerman 1999), a significant limitation on her ability to choose mates in large aggregations. The effects of background sound should also affect discrimination as well as detection of signals, but this effect has seldom received attention (Schwartz & Gerhardt 1989, 1998).

In tasks requiring only detection of signals, there is no choice among signals. Detection occurs when a receiver determines whether or not a signal has occurred and responds appropriately. There are four possible outcomes: responding when an appropriate signal is present (correct detection) or absent (false alarm) and not responding when an appropriate signal is present (missed detection) or absent (correct rejection). Of these four possibilities, two represent errors (false alarm and missed detection).

In tasks requiring discrimination, the receiver must choose among multiple signals. A receiver must thus determine which, if any, signal has occurred and respond appropriately. The possibilities for error multiply to include responding to one signal as if it were another, as well as responding in the absence of any signal or not responding at all in the presence of either signal. In this case there are nine possible results, seven of which are errors.

Discrimination is thus a more demanding task than detection alone. Experiments with human observers confirm predictions from signal detection theory that error rates at any level of background noise are higher for tasks requiring discrimination than for those requiring only detection (Starr et al. 1975; Swets et al. 1978). In other words, subjects cannot effectively discriminate signals even when they can detect them. In the experiment reported here, we examine females' abilities to discriminate among advertisement calls of conspecific males in the presence of natural background sound.

Our subjects, *Hyla ebraccata*, are small frogs numerous in the rainforests on the Caribbean slope of Central America (Duellman 1970). Whenever rain is sufficient, males congregate in emergent aquatic vegetation and call to attract mates (Duellman 1967, 1970; Donnelly & Guyer 1994). Gravid females arrive later in the evening, move cautiously through the chorus, and eventually approach a calling male. A male initiates amplexus when a female comes close, and the female then carries him to a site suitable for oviposition.

In standard experiments with loudspeakers, gravid female *H. ebraccata* prefer male advertisement calls over aggressive calls, longer advertisement calls over shorter ones, and more rapid rates of calling (Wells & Bard 1986). Females also preferentially approach calls with pulse repetition rates at the population mean rather than those with higher or lower rates (Wollerman 1998). Like some other anurans, they also prefer calls with low carrier frequencies (2960 Hz, the fifth percentile of the

population) over those at the population mean (3240 Hz) (Wollerman 1998).

Previous experiments have investigated females' abilities to detect males' advertisement calls in background noise (Wollerman 1998). These experiments presented calls with carrier frequencies of 3240 Hz in the presence of noise from a natural chorus in Costa Rica. Loudspeakers broadcasting background sound mixed with a single male's calls at signal/noise ratios of 3 dB or higher were preferred over those broadcasting background sound only. A signal/noise ratio of 3 dB is thus the threshold for detection of an individual male's calls in a natural chorus.

The experiment reported here examined the behaviour of females in the more difficult task of discriminating between calls with different carrier frequencies in the presence of natural background sound from a large chorus. We compared females' responses to loudspeakers broadcasting individual males' calls with carrier frequencies of 2960 and 3240 Hz in four conditions of background noise (signal/noise ratios of 3, 6, 9 and approximately 25 dB). The results confirm the expectation that, with enough background sound, female frogs do not discriminate between otherwise preferred and unpreferred conspecific calls even when they can detect them.

METHODS

Experimental Procedures

We conducted this study at La Selva Biological Station, Costa Rica, in July and August 1994 (experiments with signal/noise ratios of 25 and 3 dB) and in July and August 1995 (experiments with signal/noise ratios of 25, 9 and 6 dB). Gravid females, identified by the presence of eggs, were collected between 2000 and 2400 hours from a seasonal marsh (Experimental Swamp I) located at approximately 250 m north on the Camino Experimental Sur. Experiments were conducted between 2230 and 0600 hours in a laboratory with screened windows and thus conditions similar to those in the ambient environment. Temperature in the laboratory ranged from 24 to 26°C with ambient noise levels of 50–55 dB (sound pressure level (SPL) measured with Extech Instruments 407735 meter, fast response, flat-weighting). The experimental arena, constructed of foam padding 75 mm thick, was 1 m wide by 2 m long and identical to ones used in previous experiments (Wollerman 1998). It was lit by a dim red bulb located on one side midway between the speakers. We tested all females during the night in which they were collected and released them by dawn.

We offered females a choice between two calls that differed in dominant frequency (2960 and 3240 Hz) at four signal/noise ratios (25, 9, 6 and 3 dB). We placed females in a box (80 × 60 × 50 mm) constructed of screen in the centre of the arena and allowed them to listen to stimuli broadcast from the speakers for 1–2 min. Then, using a string attached to the lid of the box, we removed the lid and allowed the female 10 min to leave the box. We gave them 10 min to approach a speaker

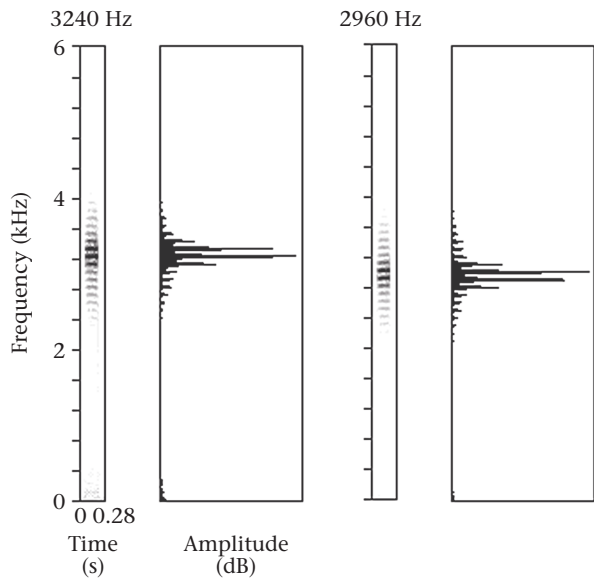


Figure 1. Spectrogram (left) and power spectrum (right) of the 3240 and 2960 Hz computer-synthesized calls used in discrimination experiments.

within 25 mm. Females typically performed behaviours indicative of phonotaxis such as zigzag jumping and head scanning (Gerhardt 1995). If a female did not leave the box within 10 min or did not choose a speaker within 10 min after leaving the box, we retested her later in the evening, if time permitted.

We played stimulus tapes on either a Sony TC-D5M or a Marantz PMD 440 recorder, amplified with Amplivox Model S702 amplifiers, and broadcast with Realistic Optimus Pro-7 speakers. The frequency response of the speakers was flat (± 3 dB) over the range of frequencies important to this experiment (100–6000 Hz). For the 25 dB signal/noise ratio, we broadcast computer-synthesized calls at 78 ± 1 dB SPL (1994) or at 80 ± 1 dB SPL (1995; peak hold, flat weighting in both years) without chorus noise added. For all choice tests with chorus noise added (9, 6 and 3 dB signal/noise ratios), we adjusted the SPL of the chorus from each speaker to 74 ± 1 dB (fast response, flat weighting). When both speakers broadcast chorus noise, we increased the SPL of the background noise by 3 dB to 77 ± 2 dB, to produce the appropriate signal/noise ratio (see Playback Tapes). We measured all sound pressure levels at the centre of the arena, where females were released. We alternated the location of each stimulus in successive tests.

Playback Tapes

Playback tapes consisted of 30 min of computer-synthesized calls (2960 or 3240 Hz) recorded at a typical call repetition rate (10 calls/min). For details of call synthesis, see Wollerman (1998). We checked computer-synthesized calls (Fig. 1) for spectral and temporal accuracy by comparing them to natural calls with a Uniscan II real-time spectrum analyser and SuperScope digital oscilloscope software on a Macintosh 68030 computer.

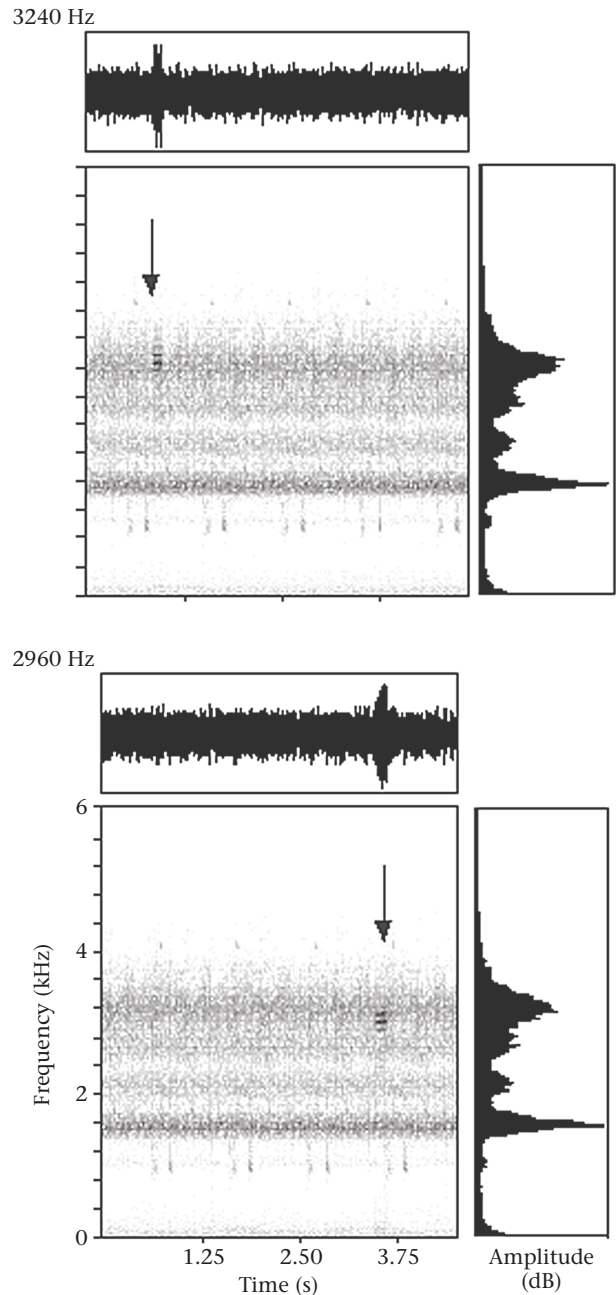


Figure 2. Oscillograms (above), spectrograms (below, left) and power spectra (below, right) of the noise plus signal playback tapes used in discrimination experiments. This figure shows the +3 dB signal/noise ratio. The location of the signal is indicated by the arrow.

We recorded chorus noise from the study site in 1993 (Fig. 2). We digitized a short (approximately 1 s) segment of chorus that lacked any distinct *H. ebraccata* calls with an Audiomeia A/D card on a Macintosh 68030 computer (16-bit precision, 16 kHz sampling rate) and then duplicated this segment to produce 30 min of chorus sound with a nearly constant amplitude. This chorus noise was band-passed (250–5000 Hz, 24 dB/octave, Krohn-Hite brand filter model number 3700) and recorded on a Marantz PMD 440 tape recorder through the Macintosh

sound port (8-bit precision, 48 dB signal/noise ratio).

For signal/noise ratios of 9, 6 and 3 dB, we mixed the signal (a computer-synthesized call of either 2960 or 3240 Hz) and the chorus noise by monitoring the amplitude of the output of a Realistic 1200c stereo mixer with an oscilloscope. To determine the appropriate amplitude for the chorus relative to the signal, we used the following procedure. During playbacks, chorus noise broadcast simultaneously from two speakers equidistant from the centre of the arena increased in intensity by 3 dB. Because calls from the two speakers did not overlap, no increase in intensity of the signal occurred. Therefore, to conduct a playback with a signal/noise ratio of 3 dB, we created a tape with a signal/noise ratio of 6 dB (the amplitude of the chorus noise was 50% of the call amplitude). When broadcast from both ends of the arena, the chorus noise increased by 3 dB and the resultant signal/noise ratio was 3 dB. After the appropriate signal/noise ratio for each tape was obtained, the output of the mixer was band-passed (250–5000 Hz, 24 dB/octave, Krohn-Hite brand filter model 3700) and recorded with a Sony TC-D5M tape recorder. No chorus noise was added to the tapes used with the 25 dB signal/noise ratio. We checked tapes for equality of signal/noise ratio by ear in an arena similar to the one used in female choice experiments.

Data Analyses

In 1994, we tested 13 females with both signal/noise ratios (25 and 3 dB). Half of the females were tested with the quiet conditions (25 dB signal/noise ratio) first, the other half were tested with the noisy conditions (3 dB signal/noise ratio) first. In 1995 we tested 48 females, 16 at each signal/noise ratio (25, 9, or 6 dB). We tested preferences for statistical significance with two-tailed log-likelihood ratios (G tests). We compared the results from the 9, 6 and 3 dB signal/noise ratios to those from the 25 dB signal/noise ratio with one-tailed Fisher's exact tests. One-tailed tests were appropriate because background noise is not expected to enhance discrimination. We compared the time that females took to leave the box, the time they took to choose a speaker, and their path lengths during trials in the different signal/noise ratios with one-way analysis of variance (ANOVA).

RESULTS

With the 25 dB signal/noise ratio, females preferred the speaker broadcasting the computer-synthesized call with a carrier frequency of 2960 Hz in both years (G test: 1994: $G_1=4.8$, $N=11$, $P=0.028$; 1995: $G_1=4.2$, $N=16$, $P=0.041$; 1994 and 1995 combined: $G_1=8.33$, $N=27$, $P=0.003$; Fig. 3). Females had no significant preference for either stimulus in the two intermediate signal/noise ratios (9 dB: $G_1=0.83$, $N=11$, $P=0.363$; 6 dB: $G_1=0.00$, $N=8$, $P=1.000$; Fig. 3). In the lowest signal/noise ratio, females preferred the 3240 Hz call (3 dB: $G_1=4.8$, $N=11$, $P=0.028$; Fig. 3), contrary to their preference in quiet conditions. The results of the 25 and the 3 dB signal/noise ratios were significantly different from one another (one-tailed

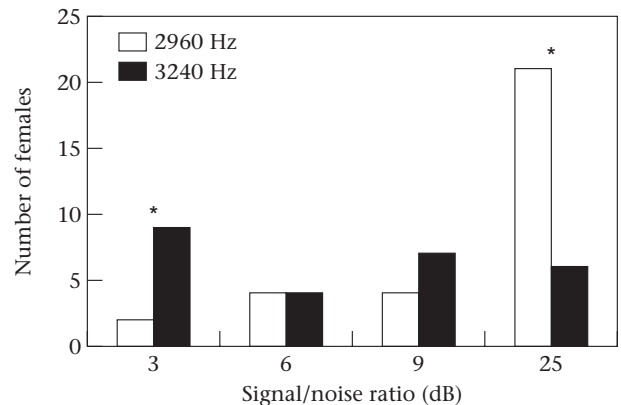


Figure 3. Results of female choice tests in the presence of acoustic interference. *Indicates significant differences ($\alpha=0.05$). Sample size for 25 dB signal/noise ratio ($N=27$) represents the combination of results from 1994 ($N=11$) and 1995 ($N=16$).

Fisher's exact test: $N=22$, $P=0.004$). The 9 dB signal/noise ratio was marginally different from the 25 dB signal/noise ratio (one-tailed Fisher's exact test: $N=27$, $P=0.054$), but the 6 dB signal/noise ratio was not different from the 25 dB signal/noise ratio (one-tailed Fisher exact test, $N=24$, $P=0.221$).

We found no other effects of the signal/noise ratio on females' behaviour. Females took significantly longer to leave the box in the 25 dB signal/noise ratio in 1995 than in 1994 (one-way ANOVA; $F_{1,28}=19.818$, $P<0.001$; Fig. 4a), but signal/noise ratio did not affect this latency within either year (one-way ANOVA: 1994: $F_{1,24}=1.26$, $P=0.273$; 1995: $F_{2,42}=1.591$, $P=0.216$; Fig. 4a). There were no differences between years in how long females took to choose a speaker once they left the box (25 dB, one-way ANOVA: $F_{1,25}=0.794$, $P=0.382$). The time that females took to choose a speaker was also unaffected by signal/noise ratio (one-way ANOVA: $F_{3,52}=0.133$, $P=0.940$; Fig. 4b). Furthermore, choosing and nonchoosing females did not differ in how long they took to leave the box in any signal/noise ratio (Fig. 5).

The path lengths of females who chose a speaker were significantly shorter than those of females who did not (one-way ANOVA: $F_{1,68}=29.243$, $P<0.001$). However, path lengths of females were not affected by the signal/noise ratio, either for females who chose a speaker (one-way ANOVA: $F_{3,52}=0.446$, $P=0.721$; Fig. 6) or for those who did not (one-way ANOVA: $F_{3,10}=0.232$, $P=0.872$; Fig. 6). In all signal/noise ratios, some females did not choose a speaker within the allotted time. There was no significant relationship between proportions of females choosing a speaker and signal/noise condition (Pearson correlation: $r_2=0.493$, $P=0.507$, two-tailed test).

When we tested females twice (in 1994), five of the females chose the same call in both tests and five of the females chose different calls (three made no choice in one of the tests). Females tested in 25 dB signal/noise condition first seemed no more or less likely to choose the same call than females tested in the 3 dB signal/noise condition first (sample sizes were too small for statistical analysis). In all signal/noise ratios, some females failed to respond

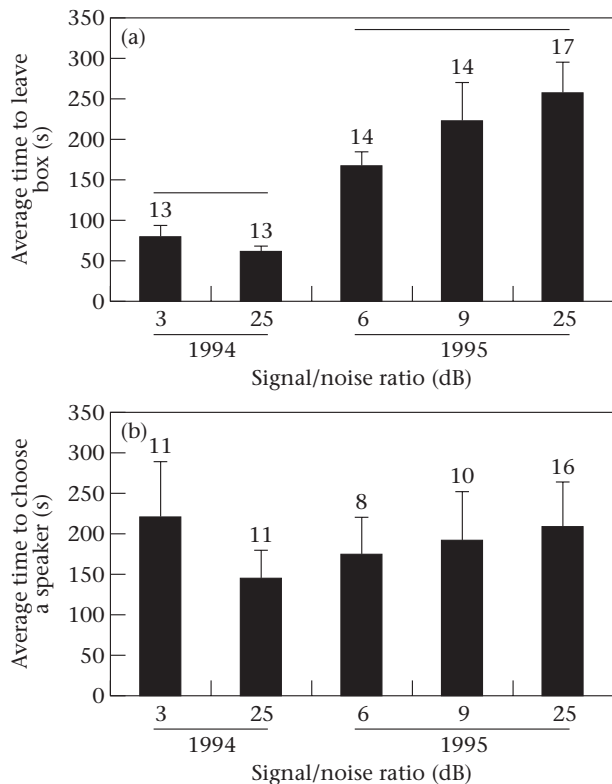


Figure 4. (a) Average time (+SE) for females (choosing and nonchoosing females combined) to leave the holding box during playback experiments. The bars connect nonsignificant differences. No between-year comparisons were made. (b) Average time (\pm SE) for females to choose a speaker in playback experiments. There were no significant differences in any comparison. Numbers above bars are sample sizes. Sample sizes in (a) and (b) differ because not all females who left the box ultimately chose a speaker.

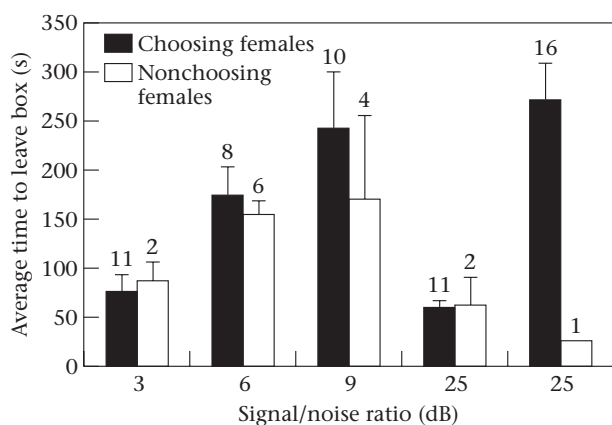


Figure 5. Average time (+SE) for choosing and nonchoosing females to leave the holding box. Within each signal/noise ratio, there were no significant differences between choosing and nonchoosing females. No statistics were calculated for the 25 dB (1995) signal/noise ratio. Numbers above bars are sample sizes.

in a trial and some of these females were retested later in the evening. Most of these females responded when retested, but the small sample sizes precluded any comparisons of retests (Table 1). Thus signal/noise ratio

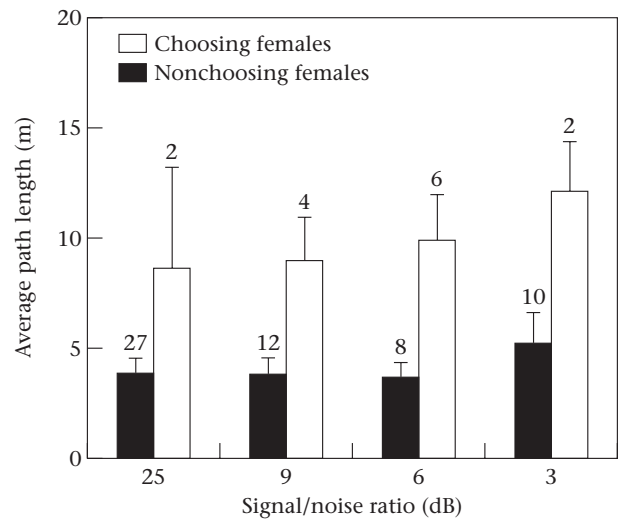


Figure 6. Path length (average +SE) of females in the different signal/noise conditions. Signal/noise ratio had no effect on path length for females who chose a speaker nor for females who did not. Choosing females (all signal/noise ratios combined) had shorter path lengths than nonchoosing females (all signal/noise ratios combined). Numbers above bars are sample sizes.

had no discernable effect on activity of females during playback tests other than their ability to discriminate between the two signals.

DISCUSSION

Discrimination by Females in Noise

Our results show that background sound from a natural chorus affects the ability of female *H. ebraccata* to discriminate among conspecific male calls. As predicted by signal detection theory, discrimination (making a choice between two alternative signals) was more difficult than detection (making a choice between signal and no signal). In conditions with no added background noise (25 dB signal/noise ratio), females preferred calls with a carrier frequency of 2960 Hz over those with a carrier frequency of 3240 Hz (as reported in separate experiments by Wollerman 1998). Similar experiments have also shown that females detect a single conspecific call provided it is at least 3 dB more intense than background sound from a chorus (Wollerman 1999). Yet the present experiment indicates that females do not discriminate between preferred and nonpreferred conspecific calls even with a 9 dB signal/noise ratio.

Females in noisy conditions might avoid making any choice and instead wait for more favourable conditions. This possibility does not seem probable for *H. ebraccata* at our study site. More females visited the chorus on noisier nights than on quieter ones (L. Wollerman, personal observation), so they did not appear to avoid high background noise. In addition, females' motivation did not appear to differ among the acoustic conditions in the present experiment. There was no effect of signal/noise condition on the proportions of females that made a choice, the time required to leave the starting box, or the

Table 1. Responses of females who were retested because they did not respond in their first trial

Signal/noise ratio	Number not choosing	Number retested	Number choosing 2960 Hz call	Number choosing 3240 Hz call
25 dB	3	2	1	1
9 dB	4	3	1	1
6 dB	8	5	1	2
3 dB	2	0		

time required to meet the criterion for choosing a speaker. In fact the tendency (although not statistically significant) was in the opposite direction, towards quicker choices in noisier conditions, as if greater acoustic stimulation might have facilitated instead of inhibited mate choice. A lack of motivation thus does not explain the failure of our subjects to discriminate between preferred and unpreferred calls in noisy conditions.

Another possibility in experiments like this one is the chance that added noise would mask the two signals to different degrees. If so, differences in the detectability of the two signals could explain females' preferences. For instance, female spring peepers, *Pseudacris crucifer*, prefer calls with higher carrier frequencies in the presence of background noise but not in quiet conditions (Schwartz & Gerhardt 1998). Because differences in masking of the signals in their study could produce the same result, it is not clear whether or not females' ability to discriminate between the two signals actually changed.

In our experiments, on the other hand, any differences in masking of the two signals by the background noise cannot explain the decreased discrimination in noisy conditions. As evident from Fig. 2, any such differences in masking would have increased rather than decreased the salience of the 2960 Hz signal and thus would have increased the chance that this signal would have been preferred in noisy as well as in quiet conditions.

The conclusion thus seems robust that background noise from a natural chorus reduced a female's ability to discriminate between preferred and unpreferred conspecific calls, even when detection was not a problem.

Change of Females' Tactics

The results also indicate that background sound altered a female's tactics for mate choice. With the lowest signal/noise ratio, females chose calls with a carrier frequency near the population mean more often than calls with a lower frequency, a reversal of the situation without added noise. This tendency also appeared in the other noisy conditions, although not significantly so.

In noisy conditions, females avoided the subtleties of discriminating among calls of conspecific males and instead chose calls near the population mean. This change would decrease the chances of mating with a heterospecific male when responses were prone to error. By attending to fewer alternatives, female behaviour became equivalent to a shift from discrimination to detection. In noisy conditions they thus abandoned the

more difficult task of discriminating among multiple alternative conspecific males and reverted to the simpler task of detecting a typical conspecific male, one with modal properties for the population.

In natural conditions, females might revert to detection at some distance from a chorus, where discrimination among conspecific males is less critical. Even after a female has entered a chorus, she is unlikely ever to hear more than one male at a time with signal/noise ratios greater than 9 dB, and even then only at very close range (Wollerman 1999). Consequently, if females were to discriminate between preferred and unpreferred conspecifics in natural conditions they would have to do so sequentially rather than simultaneously. We need more studies of sequential discrimination in this and similar species.

There are thus two ways to understand the females' change in behaviour. A functional explanation focuses on the advantages to females in different situations, such as different distances from calling males. A signal detection explanation focuses on the limitations imposed by different situations on the possibilities for communication. These are not alternative hypotheses but different components of a complete understanding of the evolution of communication. Limitations on signal detection impose general constraints within which communication adapts to particular situations.

Discrimination by Females in Aggregations

Even without added noise, the number of choices a female faces influences her ability to discriminate among them. This point first became clear when Gerhardt (1982) reported that preferences of female *H. cinerea* are less consistent when they have four choices than when they have two. Similar effects are reported for the painted reed frog *Hyperolius marmoratus* (Telford et al. 1989) and midwife toads *Alytes obstetricans* and *A. cisternasii* (Márquez & Bosch 1997). Increasing the number of possible signals increases the uncertainty that any one signal will occur and thus reduces its discriminability, a result predicted from signal detection theory and confirmed for human subjects (Nolte & Jaarmasa 1967; Starr et al. 1975; Swensson & Judy 1981). Discrimination of conspecific calls by female frogs is thus affected by the number of discriminations she makes, as well as by the level of background noise.

Both of these results call into question a common explanation for the formation of mating aggregations

such as frog choruses, on the grounds that aggregations facilitate comparisons among potential mates. Experiments with multiple choices and with natural levels of background noise show that this assumption is oversimplified. Aggregations can facilitate discrimination by allowing direct comparisons among signals, but the inevitable multiplication of choices and increase in background noise also hinder discrimination. Recent theory has shown that females' errors have pronounced influences on the distribution of matings in aggregations (Johnstone & Earn 1999). This theory has assumed fixed levels of female error, although the effects of background noise and multiple choices make it likely that female error instead increases with the size of an aggregation.

Evolution of Communication in Noisy Environments

As the present experiments emphasize, receivers rarely have perfect information about the presence or nature of signals, and this uncertainty is likely to be high in the presence of background energy or competing signals. The task of detecting one kind of signal in a noisy environment has four possible outcomes, two of which are errors. In more complicated tasks, such as discrimination between two or more signals, the possibilities for error multiply. A receiver might correctly detect and classify a signal, but it might also erroneously classify a signal after correctly detecting it, or it might fail to detect a signal altogether. When discriminating between two possible signals in noise, a receiver faces nine possible outcomes, only two of which represent correct detection and classification of a signal (McNicol 1972; MacMillan & Creelman 1991; Wiley 1994).

It is clear that the probabilities of each of these outcomes are related (Wiley 1994). When uncertainty is high, a receiver is unlikely always to respond appropriately when a particular signal is present without sometimes responding when the signal is absent. Nor is a receiver likely always to avoid responding to inappropriate signals without sometimes missing an appropriate one. A receiver thus inevitably faces trade-offs among the multiple possible outcomes of any decision to respond or not to respond. In these conditions, the criterion for response should evolve to optimize its expected utility for receivers (Wiley 1994, 2000).

Although no experiment has yet measured all of the outcomes faced by a female frog in choosing a mate in natural conditions, the present study indicates that the possibilities for errors are likely to be large and trade-offs inevitable. Furthermore, females in noisy conditions might well change their tactics to simplify their choices and thus reduce their errors.

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