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Stabilizing and directional preferences of female *Hyla ebraccata* for calls differing in static properties

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Abstract. Female frogs of many species show preferences for calls with particular properties. This study focuses on female preferences in *Hyla ebraccata* for computer-synthesized calls that differ in pulse-repetition rate or dominant frequency. Both of these call properties are static acoustic properties of advertisement calls of *H. ebraccata* (within-male coefficient of variation <5%). Females exerted directional selection on dominant frequency, preferring low-frequency calls (2960 Hz) to calls with the dominant frequency of the population mean (3240 Hz). Because size is negatively correlated with dominant frequency, female choice could explain size-biased mating success observed in natural populations. Females also exerted stabilizing selection on pulse-repetition rate, preferring calls with a pulse-repetition rate of the population mean (99 Hz) to calls with a pulse-repetition rate that was twice as fast (200 Hz). The results of this study show that female choice creates either directional or stabilizing selection on static properties of calls.

Female frogs use the advertisement calls of males to identify conspecifics (Blair 1955, 1958; Martof & Thompson 1957; Oldham & Gerhardt 1975; Backwell & Jennions 1993) and to choose between conspecific males (Whitney & Krebs 1975; Ryan 1980; Sullivan 1983; Wells & Bard 1986; Morris 1989; Robertson 1990; Marquez 1995). Results of research on preferences of female frogs for males' calls has only recently been placed into a context that could generate predictive hypotheses about how selection by female choice might influence call properties. Call properties can be categorized by the variability with which they are produced by individual males (Gerhardt 1991; Ryan & Wilczynski 1991; McClelland et al. 1996). Gerhardt termed properties with low levels of variability (within-male coefficients of variation <5%) 'static' and those produced with higher variability 'dynamic'. Both terms, however, represent only two categories in a continuum of variability, with some organisms producing calls with properties that are intermediate between static and dynamic (Butlin et al. 1985).

Gerhardt (1991) reviewed evidence that call properties with low variability (static properties) are subject to stabilizing or weakly directional selection from female choice, with females preferring calls with values near the population mean over those with extreme values. These call characteristics are likely to be important in species identification, because female preferences for calls reflecting the population mean decrease the probability of mating with a heterospecific. Call properties with high variability (dynamic properties) are subject to directional selection from female choice (Gerhardt 1991), with females preferring calls with extreme values over those with values at or near the population mean. Both types of call properties could thus be important for female choice.

Variation in call properties might also be constrained by morphology or production abilities. In cricket frogs, *Acris crepitans*, properties of calls with low within-male coefficients of variation, such as dominant frequency, are influenced most strongly by morphology, whereas properties with high within-male coefficients of variation, such as call-repetition rate and call duration, are influenced most by physiological and behavioural mechanisms (Ryan & Wilczynski 1991; McClelland et al. 1996). This perspective is not

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necessarily incompatible with an association between call variation and female preferences. The morphology or physiology of signallers could constrain patterns of variation in call properties, and because females rely on the variability in males' calls to identify suitable mates, female choice could be constrained in turn by variability in call properties.

A dichotomy between interspecific mate choice (species recognition) and intraspecific mate choice is probably false (Ryan & Rand 1993; Wiley 1994; Wilczynski et al. 1995). Female preferences that allow species identification do not necessarily take precedence over those for particular conspecific males (Gerhardt 1991; Ryan & Rand 1993; Wilczynski et al. 1995). At times, properties used for species identification and intraspecific mate choice could be redundant (Wilczynski et al. 1995). It is also possible that selection on females to identify a conspecific mate conflicts with selection to identify an optimal mate among conspecifics. For example, in many anurans, body size of a male is negatively correlated with the dominant frequency of his calls. Thus, females could use the frequency of calls to judge the size of males. If larger males have better genes (Woodward 1987; Woodward et al. 1988; Reynolds & Gross 1992), control better resources (Howard 1978), or fertilize more eggs (Ryan 1985; Robertson 1990; Bourne 1993), then females might gain fitness from choosing a larger mate. However, this advantage of mating with extreme conspecifics could be diminished by the risk of mating with heterospecifics.

In the advertisement calls of *H. ebraccata*, dominant frequency and pulse-repetition rate have low within-male coefficients of variation (<5%). If this species fits the pattern reported by Gerhardt (1991), female choice should exert stabilizing or weakly directional selection on both parameters. Females should prefer calls with the population mean when given choices between these calls and alternatives higher and lower than the mean. Evidence from field studies suggests that female *H. ebraccata* might exert directional selection on dominant frequency. Dominant frequency of calls of *H. ebraccata* decreases as body size increases (Morris 1991), and female *H. ebraccata* mate preferentially with large males in the field (Morris 1991). Female directional preferences for males with lower-frequency calls could produce this size-biased mating. In this study, I investigated female preferences for dominant frequency and pulse-repetition rate.

METHODS

Study Site and Study Organism

I studied acoustic communication and mate choice in *H. ebraccata* at La Selva Biological Station, Costa Rica from 1991 to 1993. The study site at La Selva, Experimental Swamp I, was a large marsh situated ca 250 m N on Camino Experimental Sur. Dominant vegetation in the marsh was *Spathiphyllum friedrichsthalii* (Araceae) and *Panicum grande* (Poaceae). *Pentaclethra macrolobum* (Mimosaceae) and *Ficus* spp. (Moraceae) were the dominant trees at the edges of the marsh (Donnelly & Guyer 1994).

Hyla ebraccata is a common neotropical treefrog located throughout the Caribbean lowland rainforests of Central America, except Honduras (Duellman 1970). The males ($\bar{X} \pm$ SE snout–vent length = 25.1 ± 0.1 mm, $\bar{X} \pm$ SE mass = 0.9 ± 0.01 g, $N = 60$) call to attract females ($\bar{X} \pm$ SE snout–vent length = 31.7 ± 0.2 mm, $\bar{X} \pm$ SE mass = 2.4 ± 0.04 g with eggs, $N = 50$). *Hyla ebraccata* breed throughout the year, although reproduction is concentrated in the rainy season from May to December (Donnelly & Guyer 1994).

Male Calls

I recorded calls of 60 male *H. ebraccata* in 1991 and 1992 using a Marantz PMD 221 tape-recorder and a Sennheiser K3U/ME80 microphone. I individually marked each male by toe-clipping after I measured its body mass (to the nearest 0.05 g with a Pesola spring scale) and snout–vent length (to the nearest 0.1 mm with vernier calipers). I measured dominant frequency (the frequency containing the most energy), fundamental frequency (the lowest frequency), maximal frequency (the highest frequency), pulse-repetition rate and call duration of three calls from each male on a Uniscan II FFT real-time spectrum analyser interfaced to a 68000 microcomputer. Calls were analysed using a sampling rate of 10 kHz. Temporal measurements were accurate within 12.5 ms, spectral measurements within 80 Hz.

If calls are highly repeatable, then they could be used by females to discriminate males (Boake 1989) and influence male mating success. Thus, I compared variation in call properties within and between males in a Kruskal-Wallis one-way ANOVA. To determine whether female choice on the basis of call properties could lead to size-dependent mating success, I computed regressions of call parameters on male body mass and snout–vent length.

Experimental Procedures

I conducted female choice experiments in 1992 and 1993. Gravid females (females with eggs visible through the body wall) were collected from the study site between 2000 and 2400 hours. Experiments took place between 2230 and 0600 hours in a laboratory with screened windows, and thus in conditions similar to those in the ambient environment. Temperature in the laboratory in 1993 was 25 ± 1°C. No temperatures were recorded in 1992. All females were released by dawn, after weighing and measuring them and then marking them for individual identification (see above).

The experimental arena, with sides of foam padding (7.5 cm thick), was 1.8 m long and 1.0 m wide. It was lit by a 10-W red light bulb positioned on one side of the arena midway between the speakers. A Marantz PMD 221 and a Sony TC-D5M tape-recorder drove two Realistic amplified speakers (model 32-2031) located at opposite ends of the arena. In all experiments, the output of both speakers was equalized at 80 dB sound pressure level (SPL) at the centre of the arena with a digital sound level meter (Extech Instruments 407735, peak hold, flat response). I rechecked the SPL for each female tested.

Before I tested for preferences between calls, each female was tested for orientation to a single speaker broadcasting computer-synthesized calls. For each trial, I placed the female in a covered container (approximately 8 × 6 × 5 cm) midway between the two playback speakers from which she could hear calls broadcast from the speakers for 1–2 min. I then released the female by pulling a string attached to the lid of the container. Frogs that did not leave the container within 10 min were re-tested later in the evening, if time permitted. Each female had 10 min after leaving the container to approach within 2.5 cm of a speaker. Although phonotactic behaviour was not a criterion for choice, most females displayed such behaviours, including head-turning and crawling towards a speaker (Gerhardt 1995). Preferences were tested for statistical significance with a log-likelihood ratio (*G*-test).

In successive trials, I alternated the locations of the stimuli between two sides of the arena and, in trials with successive females, I permuted the order of the choices. To check for any preferences between speakers regardless of the stimulus broadcast, I allowed 15 females to choose between two identical calls (3240 Hz dominant frequency, 99 Hz pulse-repetition rate).

Twenty females were tested in July and August 1992 for preferences between calls that varied in their dominant frequency. Each female was offered choices between a call with the population mean (3240 Hz) and each of four alternatives (2960, 3170, 3330 and 3480 Hz). These alternatives represented the 5th, 25th, 75th and 95th percentiles of dominant frequency for the population. On average, 18 of the 20 females tested chose between the broadcast calls by approaching one speaker closely.

Females were tested in June 1993 for preferences between calls that varied in pulse-repetition rates. Each female was tested for preferences between a call with a pulse-repetition rate of 99 Hz (the population mean) and four alternatives (80, 125, 150 and 200 Hz). All calls were approximately 160 ms long. I varied the duration of pulses and intervals to create different pulse-repetition rates, so that the duty cycle remained constant. Twenty-four females were tested with pulse-repetition rates of 125 and 200 Hz and 23 females were tested with pulse-repetition rates of 80 and 150 Hz. Twenty females responded in each test. The 80-Hz pulse-repetition rate represented the 5th percentile of pulse-repetition rate for this population. The other alternatives lay outside of the range of pulse-repetition rates for *H. ebraccata* and thus represented interspecific comparisons. For example, *H. phlebodes* and *Smilisca baudinii*, two species that also call at the study site during the wet season, have mean pulse-repetition rates that fall between 150 and 200 Hz ($\bar{X} \pm$ SE pulse-repetition rate = 162.3 ± 1.1 Hz, $N = 35$ and $\bar{X} \pm$ SE = 177.8 ± 4.3 Hz, $N = 20$ respectively; Wollerman 1995).

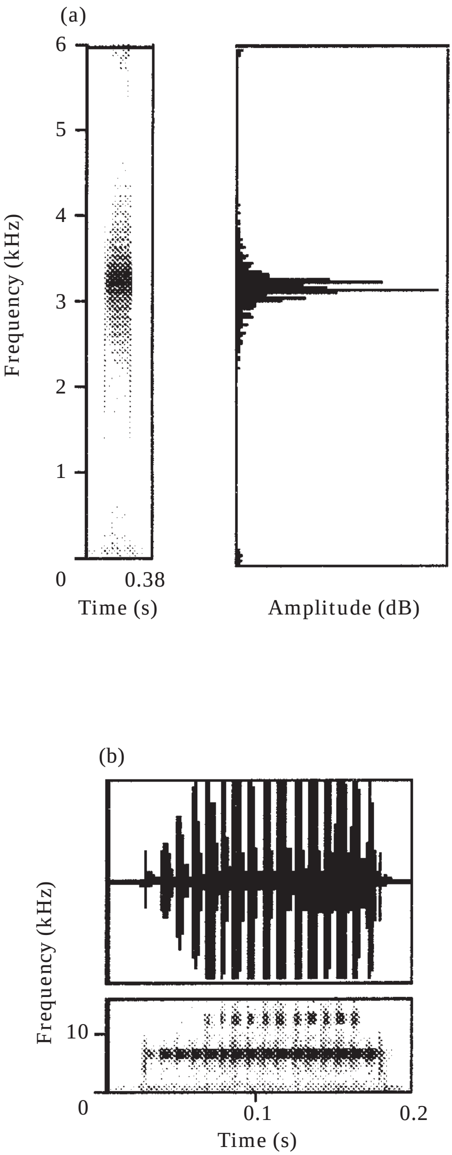

Figure 1. Spectrograms of the computer-synthesized call representing the population mean in tests of preferences between calls differing in dominant frequency and pulse-repetition rate. (a) Spectrogram (left) and power spectrum (right) of the computer-synthesized call, (b) oscillogram (above) and spectrogram (below) of the computer-synthesized call.

Playback Tapes

Playback tapes consisted of 30 min of computer-synthesized calls (see Figs 1, 2 and 3) recorded at a typical call-repetition rate (10 calls/min). To create a call, I synthesized a sinusoidal tone (22 kHz sampling rate) with SoundEdit software on a Macintosh 68030 computer. The amplitude envelope of the pulse was then modified to produce a logarithmic rise time of 1.3 ms and a linear fall time of 6.4 ms. Amplitude modulation was 100%. Pulses were joined together to create a call that was 0.16 s long, with a rise time of 50 ms and a fall time of 10 ms (Fig. 3), equal to the means for natural calls (Fig. 4). Calls were recorded on a Marantz PMD 221 tape-recorder from the Macintosh sound port (8-bit precision) after being band-passed (250–5000 Hz, 24 dB/octave) with a Krohn-Hite 3700 filter. Before using these taped calls in female choice experiments, I checked them 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 II computer).

RESULTS

Advertisement Calls

Advertisement calls of *H. ebraccata* include a primary note followed by up to six secondary clicks (Fig. 4). Calling males almost always give primary notes, but secondary clicks may or may not be added (Fouquette 1960; Wells & Greer 1981). In both years, Kruskal–Wallis tests showed that within- and between-individual variation differed significantly in dominant frequency, fundamental frequency, maximal frequency and pulse-repetition rate (Table I). In each case, there was significantly less variation within than between individual males' calls. Using averages of at least two calls (usually three) from each male, I calculated the population mean and standard deviation, and also the within-male coefficient of variation for call duration, dominant frequency, minimal frequency, maximal frequency and pulse-repetition rate of all males' calls (Table II).

There was a weak, but significant, relationship between a male's body mass and the dominant frequency of his calls (Fig. 5). Body size explains only 12% of the variation in dominant frequency; factors other than body size clearly influence the dominant frequency of advertisement calls. No other relationships between body size (mass or

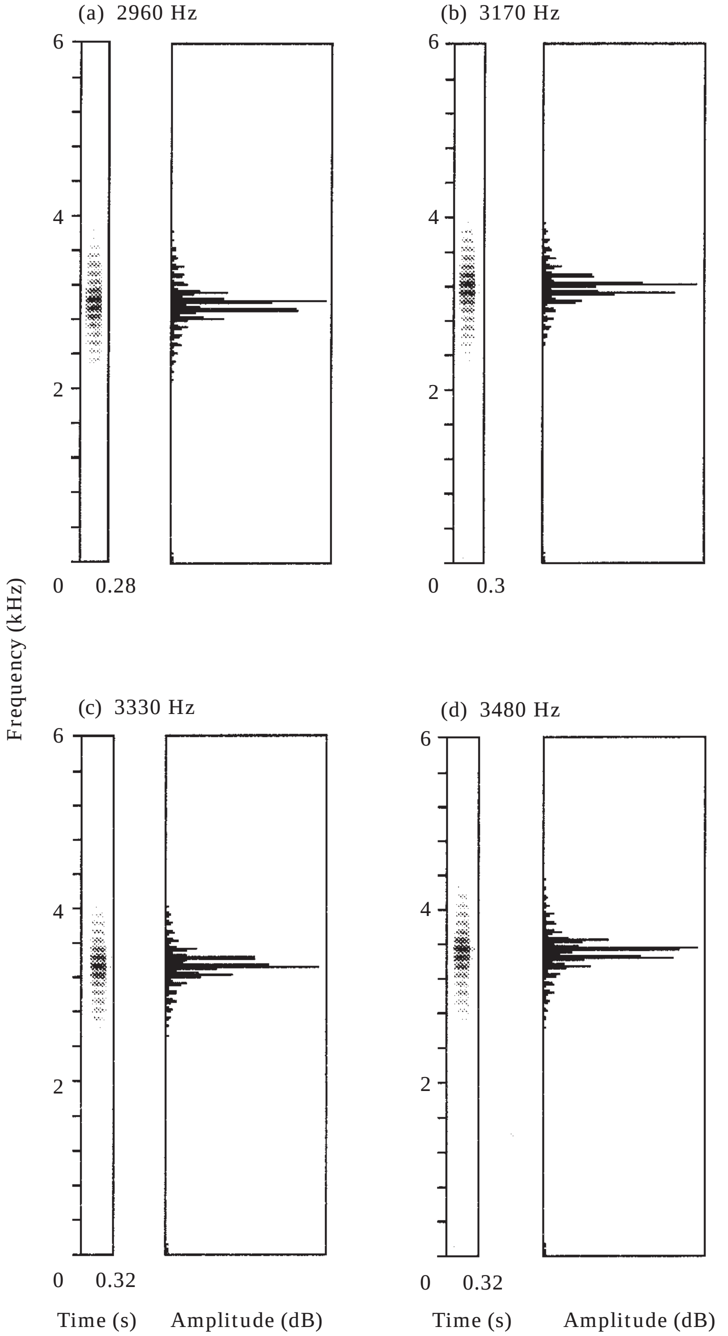

Figure 2. Spectrograms (left) and power spectra (right) of the computer-synthesized calls used in tests of preferences between calls differing in dominant frequency.

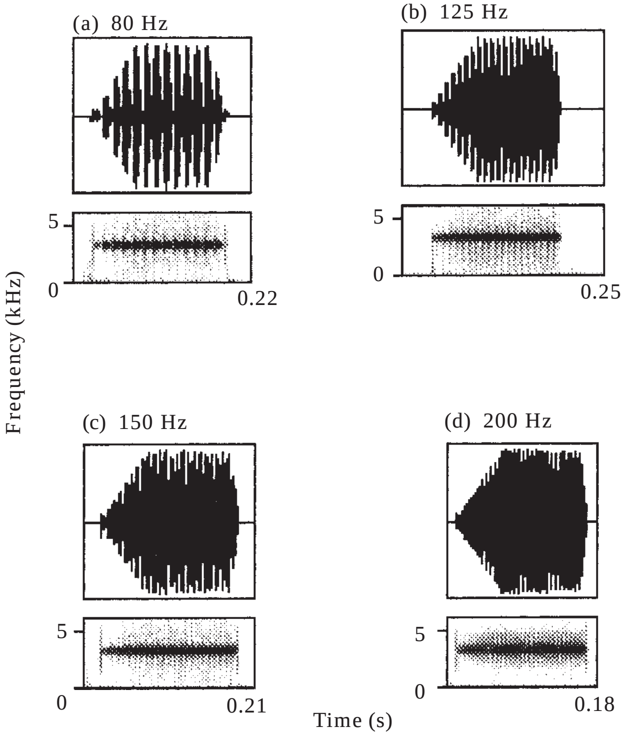

Figure 3. Oscillograms (above) and spectrograms (below) of the computer-synthesized calls used in tests of preferences between calls differing in pulse-repetition rates.

snout–vent length) and call properties were statistically significant.

Female Preferences

No preferences were observed between speakers broadcasting the same calls. Eight females chose one speaker and seven chose the other ($G_1=0.07$, $P<0.9$), so any residual differences between the speakers did not influence female choice. Subjects preferred calls with a dominant frequency of 2960 Hz to those with a dominant frequency of 3240 Hz, the population mean ($G_1=6.8$, $N=19$, $P<0.05$, Fig. 6). No other frequencies were significantly preferred over the population mean (3170 Hz, $G_1=0.9$, $N=18$, NS; 3330 Hz, $G_1=0.2$, $N=18$, NS; 3480 Hz, $G_1=0$, $N=18$, NS; Fig. 6). Females preferred calls with the mean pulse-repetition rate (99 Hz) to those with a pulse-repetition rate of 200 Hz ($G_1=7.7$, $N=20$, $P<0.01$; Fig. 7). Females also preferred the mean pulse-repetition rate in all other tests, but these results did not reach significance (80 Hz, $G_1=3.3$, $N=20$, NS; 125 Hz, $G_1=1.8$, $N=20$, NS; 150 Hz, $G_1=3.3$, $N=20$, NS; Fig. 7).

DISCUSSION

Female *H. ebraccata* can discriminate between calls on the basis of dominant frequency and pulse-repetition rate. These results raise questions about the precision of discriminatory abilities of female frogs and the possibilities for directional and stabilizing selection on features of males' calls.

There is usually a logarithmic relationship between the physical properties of a stimulus and its perception (Cohen 1984). Therefore, describing discriminatory abilities on the basis of absolute differences in frequency of the two choices probably does not accurately reflect the underlying sensory processing involved in discrimination. The ratio or the relative difference between discriminated choices, rather than the absolute difference, is more appropriate for comparing the

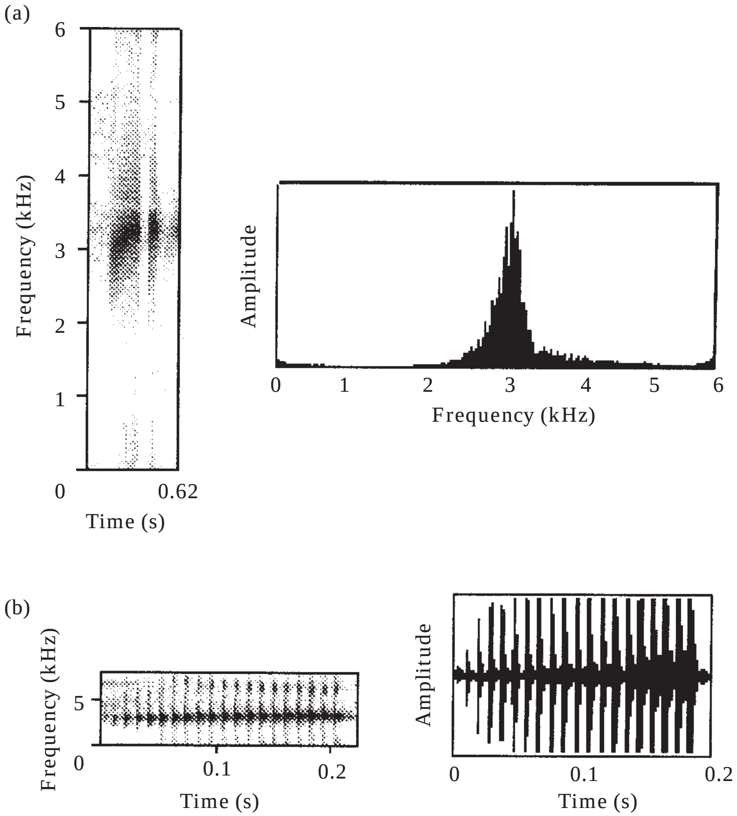

Figure 4. (a) Spectral analysis (spectrogram, left and power spectrum, right) of a natural *H. ebraccata* advertisement call. The primary note is first. (b) Temporal analysis (spectrogram, left and oscillogram right) of the primary note of a natural *H. ebraccata* advertisement call.

abilities of two species to discriminate calls that differ in frequency. Female *H. cinerea*, *H. gratiosa* and *H. versicolor* do not discriminate calls that differ by 10%. *Hyla cinerea* and *H. gratiosa*, however, do discriminate calls that differ by 20% (Oldham & Gerhardt 1975; Gerhardt 1987) and *H. versicolor* discriminates calls that differ by 15% (Gerhardt 1991). *Physalaemus pustulosus* tend to discriminate calls that differ by 30% in dominant frequency, although this result was not statistically significant (Wilczynski et al. 1995). *Uperoleia rugosa*, however, can discriminate very small differences in dominant frequency. Females discriminate calls that differ from a preferred call by as little as 1.9% (Robertson 1990). There is a 8.6% difference between calls discriminated by *H. ebraccata* (2960 and 3240 Hz). Thus, it appears that *H. ebraccata* females make finer discriminations than do some other species.

Dominant frequency and pulse-repetition rate qualify as static properties of calls having within-male coefficients of variation less than 5% (Gerhardt 1991). Female choice between calls on the basis of static properties is usually stabilizing or weakly directional (Gerhardt 1991). In *H. ebraccata*, my results for frequency discrimination indicate that female choice does not produce stabilizing selection. Although only one preference was statistically significant, females tended to prefer the alternative call to the mean dominant frequency in most tests (Fig. 6). Thus, it appears that females exert directional selection on dominant frequency of calls in this species. Whether this preference is 'weak' or 'strong', as defined by Gerhardt (1991), remains to be investigated. A weak preference is abolished by a 6-dB inequality in intensity of the two calls. If females continue to prefer the low-frequency call when it is less intense

Table I. Comparison of call properties within and between individual *H. ebraccata* in 1991 and in 1992 (Kruskal–Wallis one-way ANOVA)

Call property	*df*	Test statistic	*P*
1991			
Dominant frequency	31	80.3	<0.001
Fundamental frequency	31	88.9	<0.001
Maximal frequency	31	73.4	<0.001
Pulse-repetition rate	31	75.5	<0.001
Duration	32	51.3	0.017
1992			
Dominant frequency	26	74.6	<0.001
Fundamental frequency	26	53.5	<0.001
Maximal frequency	26	71.6	<0.001
Pulse-repetition rate	26	63.0	<0.001
Duration	26	59.3	<0.001

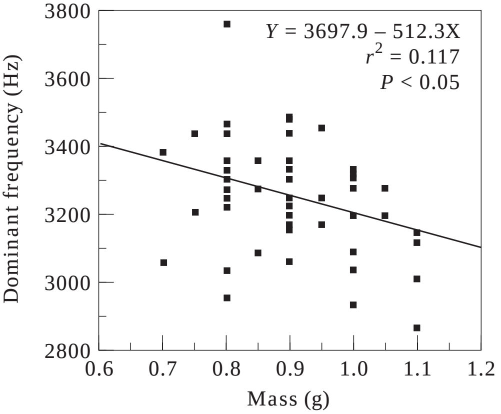

Figure 5. Regression of dominant frequency of advertisement calls on body mass of male *H. ebraccata*.

than alternatives, then this preference would be considered ‘strong’.

It is possible that females have directional preferences for dominant frequency for a number of reasons. This preference could be a result of the tuning of the peripheral nervous system of female *H. ebraccata*. The best excitatory frequency (BEF) for the basilar papilla of female *H. ebraccata* is 2077 Hz (McClelland et al. 1997), which is lower than the lowest dominant frequency offered as a choice in this experiment, or recorded from this population (unpublished data). Thus, female preference for lower-frequency calls could be explained by the sensory exploitation hypothesis of sexual selection, provided the low BEF of females is ancestral in this clade of treefrogs (Ryan 1990). In the sensory-exploitation hypothesis, male traits used in mate attraction have evolved to exploit female sensory biases that predate the evolution of the trait. Depending on the shape of the tuning curve of the basilar papilla of females, preferences for lower-frequency calls could extend to frequencies far outside the range of conspecific calls (Ryan et al. 1990, 1992). The experiments reported here, however, were conducted at sound pressure levels much higher than those used to determine the BEF in this species, so comparisons between the two studies are problematic (Gerhardt 1994).

The female preferences for low dominant frequencies and the correlation of male mass with dominant frequency together indicate that females might mate preferentially with large males. In a study of *H. ebraccata* at La Selva, Morris (1991) observed a mating advantage for large males in 1 of 3 years. My results support her suggestion that female choice was the mechanism for this nonrandom mating pattern. The inconsistency of size-related mating could be explained by the relatively weak association between male body mass and dominant frequency ($r^2=0.117$, $P=0.007$; Fig. 5) or by the success of satellite males (Miyamoto & Cane 1980). No information about the size of satellite males relative to calling males is available

Table II. Properties of the advertisement calls of *H. ebraccata* ($N=60$, recorded in 1991 and 1992)

Measure	Dominant frequency (Hz)	Fundamental frequency (Hz)	Maximal frequency (Hz)	Pulse-repetition rate (Hz)	Call duration (s)
Population mean	3256.3	2507.6	3855.8	97.2	0.162
Population SD	153.0	175.8	209.6	4.2	0.018
Average within-male coefficient of variation	1.1%	2.3%	1.8%	2.1%	6.8%

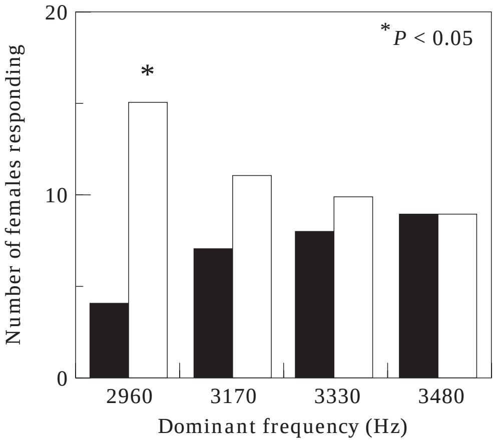

Figure 6. Results of female choice tests between calls differing in dominant frequency. ■: The population mean (3240 Hz); □: the alternatives.

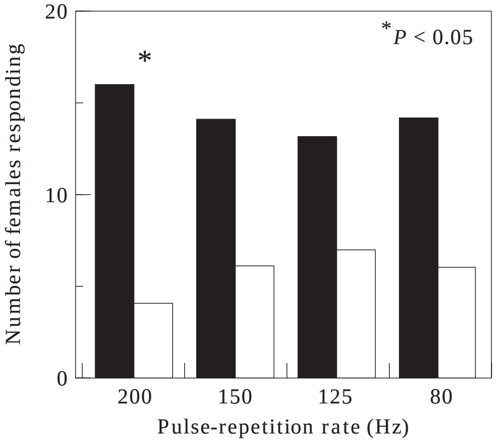

Figure 7. Results of female choice tests between calls differing in pulse-repetition rate. ■: The population mean (99 Hz); □: the alternatives.

for this species (Miyamoto & Cane 1980). If males that adopt a satellite strategy typically are smaller than the males that call on any given night (as in *H. cinerea*, Gerhardt et al. 1987), then appreciable mating success by satellite males (estimated to be 38% by Miyamoto & Cane 1980) could obscure female preferences for larger males.

Females might prefer larger males because they provide better genes for females' offspring (Woodward 1987; Woodward et al. 1988; Reynolds & Gross 1992) or fertilize eggs more efficiently (Ryan 1985; Robertson 1990; Bourne 1993). It is unlikely that other non-genetic benefits are important in this species; males do not defend territories and pairs deposit eggs away from male calling sites (Morris 1991).

Inspection of amplitude spectra of the computer-synthesized calls used in the frequency-discrimination tests shows asymmetries in the relative amplitudes of the side bands (Figs 1, 2). The 2960-, 3170- and 3480-Hz calls have a major side band just above the dominant frequency, whereas the 3170- and 3240-Hz calls have a major side band just below the dominant frequency. These side bands might have shifted the average spectral energy to a frequency lower or higher than the carrier frequency. It is unlikely, however, that these side bands influenced the outcome of female choice experiments because they are very close in frequency to that of the carrier.

In contrast to the results for choice of dominant frequencies, females' choices between calls that differed in pulse-repetition rate appeared to exert stabilizing selection on this static property. Females invariably tended to prefer the population mean over alternatives (Fig. 7). Again, it is not known whether these preferences are strong or weak.

Preferences for the mean pulse-repetition rate suggest that females might use this property to reject calls of heterospecific males. *Hyla microcephala* females discriminate conspecific calls from those of *H. ebraccata* on the basis of pulse-repetition rates; indeed, they reject calls with pulse rates typical of *H. ebraccata* (95 Hz) even when no other alternative is present (Schwartz 1987a). *Hyla ebraccata* and *H. microcephala* are not sympatric at La Selva, but *H. ebraccata* and *H. phlebodes* are. These two species have advertisement calls that are very similar in structure. For *H. phlebodes* at La Selva, the population has a mean pulse-repetition rate of approximately 162 Hz and a dominant frequency of about 3860 Hz (Wollerman 1995). There is little overlap between pulse-repetition rates of *H. ebraccata* and *H. phlebodes* (Wells & Schwartz 1984; Wollerman 1995), so it would be possible for female *H. ebraccata* to reject *H. phlebodes* on the basis of pulse-repetition rate alone. Nevertheless, because females do not avoid pulse-repetition rates of 150 Hz, my experiments suggest that females do not exclude all male *H. phlebodes* solely on the basis of pulse-repetition rates.

There are other differences between the calls of *H. phlebodes* and *H. ebraccata*, including dominant frequency and duration. Such redundancy in signals could improve the probability that females discriminate them (Wiley 1983). Nevertheless, female *H. ebraccata* approach natural *H. phlebodes* calls when tested in one-speaker experiments (Backwell & Jennions 1993). Even when given a choice between conspecific and heterospecific calls, female *H. ebraccata* sometimes respond to *H. phlebodes* calls (Backwell & Jennions 1993). A similar pattern is seen in *H. gratiosa* and *H. cinerea* (Oldham & Gerhardt 1975). Females of both species are attracted to a speaker broadcasting heterospecific calls if no other options are available; some females respond to heterospecific calls even when a conspecific alternative is played. Unlike *H. gratiosa* and *H. cinerea* (Mecham 1960), *H. ebraccata* and *H. phlebodes* cannot successfully interbreed (Fouquette 1960). The importance of pre-mating isolation by females' responses to advertisement calls need further investigation.

Hyla ebraccata is not as good at discriminating calls that differ in pulse-repetition rate as several other species are. *Hyla ebraccata* discriminated calls that differed in pulse-repetition rate by 100 Hz (200 and 99 Hz), but failed to discriminate calls that differed by 50 Hz (150 and 99 Hz). *Hyla versicolor* can discriminate differences of as little as 10 Hz (preferring 10-Hz calls to 20-Hz calls, Gerhardt 1991). *Hyla microcephala* can discriminate differences in pulse-repetition rates of 75 Hz (preferring 225 Hz to 150 Hz, Schwartz 1987a). It is surprising that *H. ebraccata* appears to discriminate calls with different temporal properties so poorly. It is possible that they are able to discriminate natural calls better than computer-synthesized calls (Robertson 1990).

Many studies of female choice have found preferences between calls only when the difference between calls was large (e.g. Arak 1988; Morris 1989). While this design yields useful information about anuran psychoacoustics, signal processing and sexual selection by female choice, it does not necessarily clarify communication or sexual selection in natural conditions. The choices that I offered and the choices offered in other studies (references in Gerhardt 1994), approximate those available in natural situations. Nevertheless, there still remain problems in applying laboratory experiments to questions about the intensity and direction of sexual selection. Too little is known about female search patterns and thresholds for mate acceptance in the field (Real 1990, 1991) to make predictions about how female preferences in laboratory experiments translate to mate choice in the field.

For many species, the most accurate predictors of male mating success are not call properties but male behaviour, such as rates of calling and persistence of attendance at choruses (Greer & Wells 1980; Kluge 1981; Sullivan 1982, 1983; Ryan 1985; Wells & Bard 1986; Gerhardt et al. 1987; Arak 1988; Morris 1989; Bourne 1992). These behaviour patterns are energetically expensive (Bucher et al. 1982; Given 1988; Wells & Taigen 1989), so these traits are measures of male vigour. In some of these species, however, females also discriminate between calls in laboratory experiments (*P. pustulosus*, Ryan 1985; *H. cinerea*, Gerhardt 1991; *H. chrysoscelis*, Morris 1989; *H. ebraccata*, this study).

To understand how female discrimination of calls is related to male mating success, we need to combine information about female discrimination in realistic, but controlled, environments with information about male mating success. A step towards understanding female discrimination in more complex environments might involve experiments with more than two alternative choices (Gerhardt 1982; Schwartz 1987b), overlapping and non-overlapping signals (Schwartz & Wells 1983; Schwartz & Rand 1991) and the addition of background noise (Gerhardt & Klump 1988; Schwartz & Gerhardt 1989; Wollerman 1995). In addition, we need to know more about the kinds of acoustic environments that females experience. Together, such research can help us to understand how choices such as those documented here are affected by competing sounds from the environment.

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