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Generalization in Response to Mate Recognition Signals

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ABSTRACT: Females usually exhibit strong and unequivocal recognition of conspecific mating signals and reject those of other sympatric heterospecifics. However, most species are allopatric with one another, and the degree to which females recognize mating signals of allopatric species is more varied. Such mating signals are often rejected but are sometimes falsely recognized as conspecific. We studied the dynamics of mate recognition in female túngara frogs (*Physalaemus pustulosus*) in response to a series of calls that were intermediate between the conspecific and each of five allopatric-heterospecific calls: two that elicited recognition from females in previous studies and three that did not. This study shows that females perceive variation in allopatric mating signals in a continuous manner with no evidence of perceptual category formation. The strength of recognition is predicted by how different the target stimulus is from the conspecific call within a series of calls. But the differences in recognition responses among call series are not predicted by the similarity of the call series to the conspecific call. The latter result suggests that the strength of recognition of allopatric signals might be influenced by processes of stimulus generalization and past evolutionary history.

Keywords: generalization gradients, mate recognition, preference functions, sexual selection, species recognition, túngara frogs.

Mate recognition is central to the process of speciation (Dobzhansky 1940; Mayr 1963; Blair 1964; Williams 1966; Andersson 1994; Ptacek 2000). In sympatry the reproductive failures often associated with heterospecific matings generate strong selection on females to mate exclusively with conspecifics. Consequently, females usually exhibit a strong preference for the conspecific mating signal over heterospecific signals, and they usually do not recognize heterospecific signals as indicating a potential mate (see Andersson 1994, pp. 211–223).

Most species, however, are allopatric with one another, and divergence of mate recognition systems might often, if not usually, occur in allopatry (e.g., Coyne and Orr 1997). Nevertheless, females usually still exhibit strong preferences for conspecific signals over those of allopatric heterospecifics (e.g., Pinto 1980; Kaneshiro 1983; Nevo and Capranica 1985; Ryan and Wilczynski 1988; Coyne and Orr 1989; Ryan and Rand 1995; McLennan and Ryan 1997, 1999). For example, in a study of a large number of *Drosophila* species, allopatric pairs tend to exhibit the same degree of premating isolation as sympatric pairs, given sufficient divergence time (i.e., when Nei's genetic distance $D > 0.5$; Coyne and Orr 1989, 1997). However, when presented with only an allopatric-heterospecific signal, females of various species sometimes perceive it as indicating an appropriate mate; that is, they "falsely" recognize it (Gerhardt 1974, 1982; Backwell and Jennions 1993; Ryan and Rand 1993*a*; Gerhardt et al. 1994; Munclinger and Frynta 1997; Saetre et al. 1997; Heth et al. 2001; Irwin et al. 2001). In rare cases females even prefer the allopatric-heterospecific signal to the conspecific one (e.g., Gwynne and Morris 1986; Ryan and Wagner 1987).

Why is there a preference for conspecific signals over allopatric-heterospecific ones when there has been no selection for females to make this distinction? This could result from selection having acted on two currently allopatric species when they were once sympatric. However, this seems unlikely to explain the plethora of conspecific versus allopatric-heterospecific preferences. Another class of explanation invokes pleiotropy. Selection in contexts other than mate recognition could influence a male's mating signal or a female's preference for that signal (Ryan 1990; Rice and Hostert 1993; Podos 2001). For example, selection favoring other mating decisions—such as those based on self recognition (Paterson 1985), mate quality among conspecifics (Andersson 1994), or discrimination

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against sympatric heterospecifics—could have an incidental consequence on how females respond to allopatric-heterospecific signals.

How might we explain false recognition of allopatric-heterospecific signals? A species' mate recognition signal will vary. It seems impossible that an animal's recognition system will be able to account for the precise magnitude of signal variation in the population. More probably it will recognize either a subset of the variation or potentially more of the variation than actually exists (Ryan and Rand 1993*b*). The latter case could lead to false recognition. The details will depend on how animals perceive stimulus variation. One possibility is that signal variation is perceived discontinuously and categorically (Ehret 1987). Categorical perception occurs when continuously varying stimuli are perceived as belonging to different categories and discrimination is sharper at category boundaries than within categories (Harnad 1987). If such were the case, selection for conspecific in favor of sympatric-heterospecific matings could influence the category boundaries, and allopatric-heterospecific signals might or might not just happen to fall outside of the category boundaries and thus be either appropriately rejected or falsely recognized.

An alternative explanation for false recognition is that the recognition decision could change gradually and probabilistically with signal variation as a function of the signal's similarity to the conspecific signal. In studies of human cognition, it has been noted that any object or situation experienced by an individual is unlikely to recur in exactly the same form and context. Therefore, individuals should be able to generalize the saliency associated with a specific stimulus to other, similar stimuli, and the strength of the response should vary predictably with the individual's perception of the differences between stimuli (Shepard 1987). The pattern of how the strength of the response varies as a function of stimulus variation is the generalization gradient. The response of females to allopatric-heterospecific signals could result from overgeneralization of the conspecific signal.

Another potential outcome of stimulus generalization is that females might show enhanced recognition of caricatures, stimuli that exaggerate certain features of the species-typical signal. If a caricature differs more from heterospecific signals than the conspecific signal, it might be more attractive to females (Enquist and Arak 1998). Again, there is an analogy from psychology: peak-shift displacement. As a example, a pigeon receives positive reinforcement to one wavelength of light, say 550 nm, and negative reinforcement to another, say 555 nm. If it pecks the keys in its box in the presence of one wavelength, it is rewarded with food; if it does so in response to the other wavelength, the lights in the box are turned out. After conditioning, the strengths of the pigeons' responses are measured across a variety of wavelengths. One might predict that the most vigorous key pecking would be to 550 nm, the wavelength at which the bird was rewarded, but the peak of responsiveness is shifted away from that wavelength to one that differs more than the wavelength associated with the negative reward, that is, to wavelengths shorter than 550 nm (Staddon 1975). If one applies this analogy to conspecific signals (positive reinforcement) and heterospecific signals (negative reinforcement), as did Enquist and Arak (1998), one predicts a strong response to some signals that are not conspecific but differ more than the conspecific signal from the heterospecific one—the caricature. Preference for a caricature, however, could have other explanations unrelated to conspecific-heterospecific discrimination, such as an open-ended preference favoring high-quality males (Andersson 1994).

All of the above questions about how females respond to allopatric-heterospecific mate recognition signals require a detailed examination of how female recognition covaries with stimulus variation. To aid this examination we constructed generalization gradients (Shepard 1987) or preference functions (e.g., Ritchie 1996; Wagner 1998; Gerhardt et al. 2000; Murphy and Gerhardt 2000) by quantifying the recognition responses of female túngara frogs (*Physalaemus pustulosus*) to calls that varied systematically between the conspecific call and a heterospecific call as well as caricatures of the conspecific call and the heterospecific calls. We refer to each of these series of calls as a transect, and the transect is identified by the heterospecific call it contains. We refer to the overall acoustic similarity of a test call to the túngara frog call as the acoustic distance. We represent call variation in multivariate space and refer to this plot of call variation as the acoustic landscape; we note that calls can have the same acoustic distance from the túngara frog call but reside in different parts of the acoustic landscape.

We tested the response of females to five call transects, two of which have heterospecific calls that elicited statistically significant recognition from females in previous studies and three of which did not (Ryan and Rand 1995, 1999, 2001). We use these data to address several questions. Do stimuli that differ from the conspecific call elicit recognition? Does acoustic distance from the test call to the conspecific call predict female response? Do the patterns of response suggest that females form categories of conspecific and heterospecific, as suggested by Erhet (1987), or do they exhibit more continuous variation in their response, such as a type of generalization gradient (Shepard 1987)? Does the shape of the preference function vary as a function of the acoustic landscape? Do females show enhanced response to caricatures of conspecific calls, as suggested by Enquist and Arak (1998)? Are there repeatable differences among females in their threshold for recognition? Answers to these questions, we believe, will provide some insights into how females perceive variation in mate recognition signals.

The túngara frog, *P. pustulosus*, ranges from Veracruz, Mexico, through much of the lowlands of Middle America, across the Darien Gap into Colombia, throughout the llanos of Venezuela, and into Guayana, and it is also found on the island of Trinidad. Túngara frogs are allopatric with all congeners where we study them in Panama, and in its entire range it is sympatric with only one other *Physalaemus*, *Physalaemus enesefae*, in the llanos of Venezuela (Ryan et al. 1996). *Physalaemus pustulosus* is a member of the *Physalaemus pustulosus* species group, which in addition to *P. pustulosus* consists of *Physalaemus petersi*, *Physalaemus pustulatus*, *Physalaemus coloradorum*, and Species B (Cannatella et al. 1998). Cannatella and Duellman (1984) suggest that *P. pustulosus* was never sympatric with the members of the species group west of the Andes (*P. pustulatus, P. coloradorum*, and Species B), but it is more difficult to speculate on the possibility of past sympatry with *P. petersi*, which is found throughout much of the Amazon Basin.

Our previous studies of túngara frogs have shown that females exhibit strong discrimination in favor of the conspecific call over allopatric-heterospecific and reconstructed ancestral calls in two-choice phonotaxis experiments (a conspecific preference in 35 of 36 experiments [Ryan and Rand 1995, 1999, 2001]). Yet when we tested female recognition in a one-choice stimulus test with those same calls, females often exhibited phonotaxis to heterospecific/ancestral calls; that is, they falsely recognized them as conspecific. The heterospecific or ancestor call was falsely recognized in 74% of 36 phonotaxis tests; three of the seven heterospecific (as opposed to reconstructed ancestral) calls yielded statistically significant recognition (see fig. 1 in Ryan and Rand 2001).

Material and Methods

Stimulus Construction

All of the species tested have a conspecific mating call whose main component is a frequency-modulated whine (Ryan and Rand 1993*a*). Studies of *Physalaemus pustulosus* show that the fundamental frequency of the whine is critical to elicit female phonotaxis and that the upper harmonics of the whine do not influence the female's behavior (Rand et al. 1992). We analyzed several components of the temporal waveform of the call and the spectral aspects of the whine's fundamental frequency for each species (fig. 1; table 1). The temporal variables include the call's rise and fall time and a measure of the time constant or shape of each. To estimate the shape of the rise, we measured the time from the call's onset to one-half the call's peak amplitude during the rise, and we then calculated the proportion of the total rise time from the beginning of the call to that midamplitude point. For the shape of the fall, we measured the amount of time from the call's peak amplitude to one-half the peak amplitude during the fall, and we calculated the proportion of the total fall time from the end of the call to that midamplitude point (fig. 1). Duration was not an independent call variable because it was the sum of the rise and fall time. The spectral variables we used were the maximum frequency of the whine (which sometimes differs slightly from the call's initial frequency), the final frequency of the whine, and a measure of the whine's time constant or shape, which is the proportion of time required for the call to reach midfrequency (fig. 1).

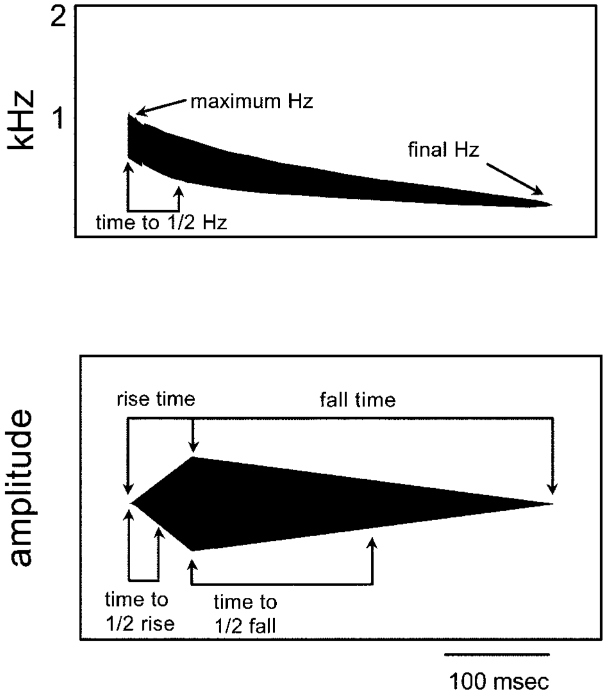

Figure 1: Illustration of the various acoustic measures made on the fundamental frequency sweep of the call of the túngara frog *Physalaemus pustulosus* and its relatives.

We used these variables to synthesize calls by digitally shaping sine waves according to the signal parameters in table 1. Previously, we tested female *P. pustulosus* with a synthetic call derived from these variables versus four natural calls. In the four simultaneous choice tests, females preferred the synthetic call in one, the natural call in another, and did not discriminate in the remaining two (W. Rand and M. J. Ryan, unpublished data). Thus, the syn-

Table 1: Average values of acoustic properties of the fundamental frequency of the whine for each species

Species	Maximum frequency	Final frequency	Rise time	Fall time	Frequency sweep shape	Fall shape	Rise shape
Physalaemus pustulosus	884	484	24.02	342.80	.33	.50	.33
Physalaemus petersi	1,220	384	13.71	230.27	.11	.80	.84
Physalaemus coloradorum	1,180	628	53.40	161.70	.38	.71	.44
Physalaemus pustulatus	964	676	99.51	104.32	.43	.49	.95
Species B	888	444	105.10	293.70	.30	.68	.66
Physalaemus enesefae	976	692	301.50	445.70	.51	.54	.55

thetic call captures the salient features necessary to support phonotaxis.

We synthesized calls that were intermediate between the conspecific call and each of five heterospecifics: Species B (this is an undescribed species and is noted as such in Ryan and Rand 1995), *Physalaemus coloradorum*, *Physalaemus enesefae*, *Physalaemus petersi*, and *Physalaemus pustulatus*. We refer to each of these series of calls as a call transect, and we label each transect by its heterospecific call. A call's position along the transect relative to the conspecific call is referred to as its acoustic distance (fig. 2). When we plot the calls in multivariate space, we refer to a call's location in the acoustic landscape, and, as above, we refer to the differences between calls in multivariate space as the acoustic distance (fig. 3). The call variables used for synthesis for each species are shown in table 1 and are derived from a previous analysis of the species' means (Ryan and Rand 1993*a*). The call similarity among the conspecific and heterospecific calls in multidimensional space is shown in figure 3, and the phylogenetic relationships of these species, from Cannatella et al. (1998), are illustrated by the branching diagrams in figures 4 and 5.

We synthesized the intermediate calls by changing each of the seven call variables in steps of one-eighth (0.125) of the total difference between the conspecific and heterospecific calls (figs. 2–4). Thus, if the call variable had a measure of 0 for the conspecific and 1 for the heterospecific, it would have values of one-eighth (0.125), two eighths (0.250), and seven-eighths (0.875) between the conspecific and heterospecific calls. This resulted in nine calls, including the conspecific and heterospecific call (figs. 2–4). Furthermore, we constructed two caricatures of the conspecific call and the heterospecific call on each transect (fig. 2). The conspecific caricatures differed by one-eighth or two-eighths from the conspecific call but differed more from the heterospecific call than from the conspecific call. An analogous situation was true for the caricatures of the heterospecific call. Following the example above, the caricatures of the conspecific call would have values of negative one-eighth (−0.125) and negative two-eighths (−0.250), and the caricatures of the heterospecific would

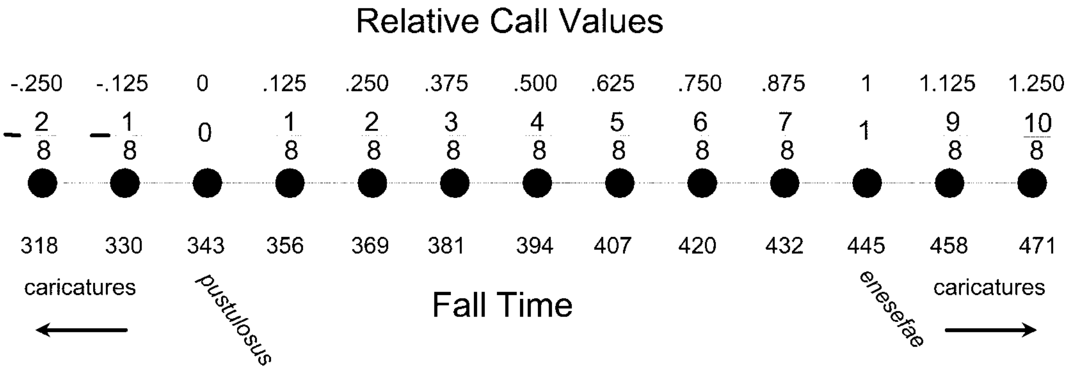

Figure 2: Illustration of a call transect. This example shows how the call's fall time varies along the transect of *Physalaemus pustulosus* to *Physalaemus enesefae*. The values of 0 and 1 are arbitrarily assigned to the conspecific (*P. pustulosus*) and heterospecific (*P. enesefae*), respectively. The fractions (shown in two forms) show the value of any call character relative to the two species' calls. Most transect call values are between the calls of the two species (i.e., 0.125–0.875), but two other sets of calls are referred to as caricatures. Conspecific caricatures (−0.125, −0.250) differ from the conspecific call value but differ more from the heterospecific, and the analogous is true of the call values of heterospecific caricatures (1.125, 1.250).

have values of one and one-eighth (1.125) and one and two-eighths (1.250). Thus, each transect had 13 calls. An example using the fall time of calls on the *P. enesefae* transect is shown in figure 2. Note that the caricatures of the conspecific call differ for each transect because the call values are dependent on the difference between the conspecific and heterospecific calls.

Phonotaxis Experiments

Females were tested for call recognition in phonotaxis experiments. There were five transects with 13 calls each, thus a total of 65 experiments. The conspecific call was tested separately in each transect to control for variation in overall female responsiveness. Twenty females were tested in each experiment; therefore, for five transects and 13 calls, there were a total of 1,300 choice tests. No female was tested more than once in the same experiment, but females were tested in more than one experiment. A total of 343 different females were tested. Most females were tested with calls from only a single transect (mean = 1.17 transects/female), and each female was tested in an average of 3.79 experiments.

We tested female túngara frogs from Gamboa, Panama, near the laboratory facilities of the Smithsonian Tropical Research Institute. Typically, females were collected at choruses between 1900 and 2200 hours and tested between 2300 and 0700 hours. Females are usually only found at a chorus when ready to mate, and most females were in amplexus (i.e., clasped by a male) when collected. After testing, females were released within 12 h of capture, which allowed them the opportunity to reproduce in the wild. They were toe-clipped so as not to be tested again in the same experiment if recaptured.

We used two acoustic chambers for the phonotaxis experiments. The first was a custom-made chamber that measured 3 × 3 × 1.78 m. During the course of these studies, this chamber was replaced by another (Acoustic Systems) that measured 1.8 × 2.7 × 1.78 m. In the first chamber, females were tested under dim red light and observed through windows in the chamber's wall. In the second chamber, the female's behavior was observed on a video monitor connected to a wide-lens video camera on the chamber's ceiling, which was equipped with an infrared light source. The females' responses did not appear to vary between chambers in these experiments.

We placed a female under a small cone in the center of the chamber; the cone could be raised remotely to initiate testing. We broadcast the test stimuli antiphonally from speakers in the center of the walls opposite one another at a peak amplitude of 82 dB SPL (re 20 μPa) and a rate of one call per 2 s from each speaker. The speaker broadcasting a stimulus was alternated between choice tests for each female. We paired the test call with a white noise stimulus of similar duration and intensity as the conspecific call. This control was necessary to eliminate the possibility that a female's response to a call was merely a more general approach to any sound. A positive phonotactic response was noted if a female approached within 10 cm of one of the speakers as long as this response did not result from the female following the chamber's walls. A female did not exhibit phonotaxis to the test stimulus if she approached the speaker broadcasting noise, if she remained motionless for the first 5 min or any subsequent 2 min of the trial, or if she did not exhibit phonotaxis after 15 min. If a female did not exhibit phonotaxis to the test stimulus, this was considered a "no response" only if she exhibited phonotaxis to a conspecific call before and after the recognition test. This control was necessary to determine if the female's lack of response was due to lack of signal saliency rather than a general lack of motivation.

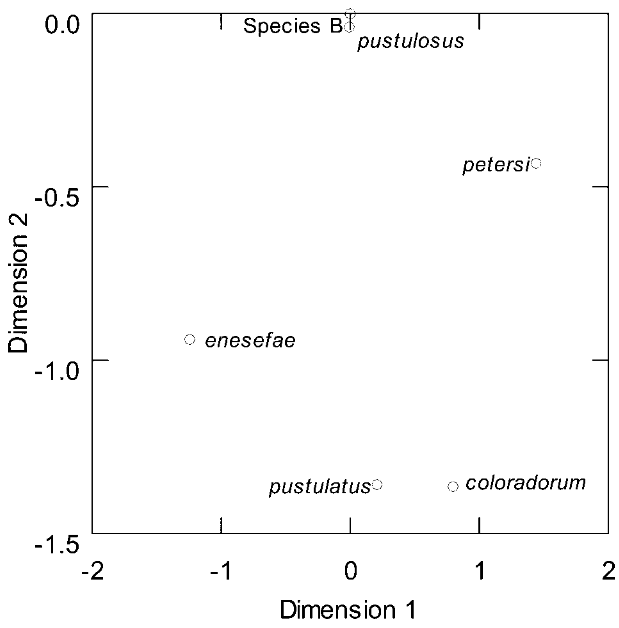

Figure 3: Multiple dimensional scaling plot of the calls of the various species used in the study. The axes plot the values of each call along the first two dimensions of the multiple dimensional scale. The values of each axis are adjusted so that the call of the túngara frog *Physalaemus pustulosus* is at coordinates 0, 0.

One of the questions we addressed was whether females respond to call variation in a categorical or continuous manner. If the former, we would expect females to have a threshold above which calls are considered conspecific and below which calls are considered not conspecific. A pattern of categorical response could be masked by individual variation among females. If females had different thresholds for their categories, the population response

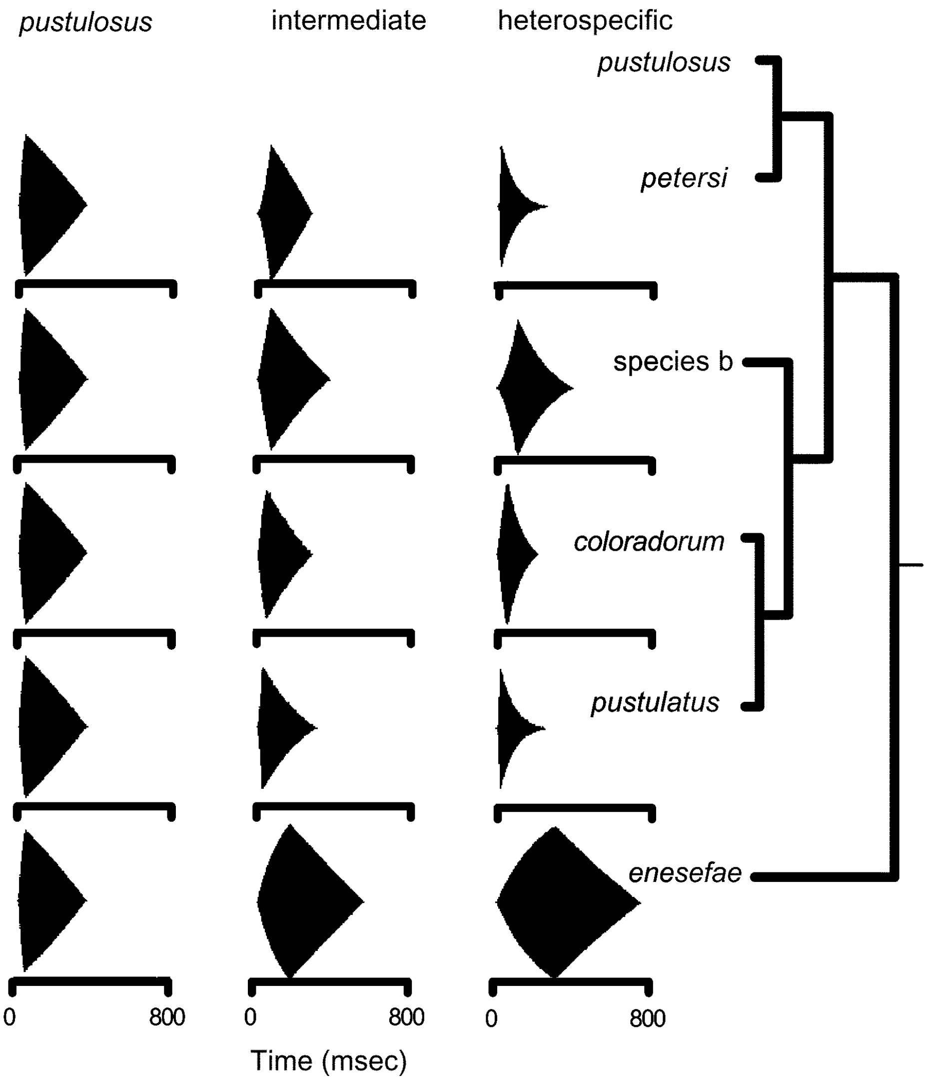

Figure 4: Oscillograms of representative calls along each of the five call transects tested in this study. The transects are referred to by the heterospecific call that they contain. We illustrate calls at transect values of 0 (which is always the *Physalaemus pustulosus* call), 1 (which is always the heterospecific call), and 0.5 (which is one of the calls with values intermediate between the conspecific and heterospecific). The branching diagram illustrates the phylogenetic relationships among the species (Cannatella et al. 1998).

might appear to be continuous. Thus, we tested the repeatability of female túngara frogs to a portion of the *P. pustulatus* transect. We tested recognition to the conspecific call (0), the heterospecific call (1), and intermediate calls of values 0.250, 0.500, and 0.750 (fig. 2). Ten females were tested five times each. The order in which females were tested with the calls in each transect series was randomized. Each female was tested with the same series five times on one night. Response criteria were as described above.

Statistics

The number of times a female would randomly contact a speaker was determined, and these data were used to formulate the null hypothesis of no response. Two of 20 females came into contact with the silent speaker (Rand et al. 1992). Thus, if females ignore the test call as a communication signal, the null expectation is that they would still approach the speaker by chance in the ratio of 2 : 18.

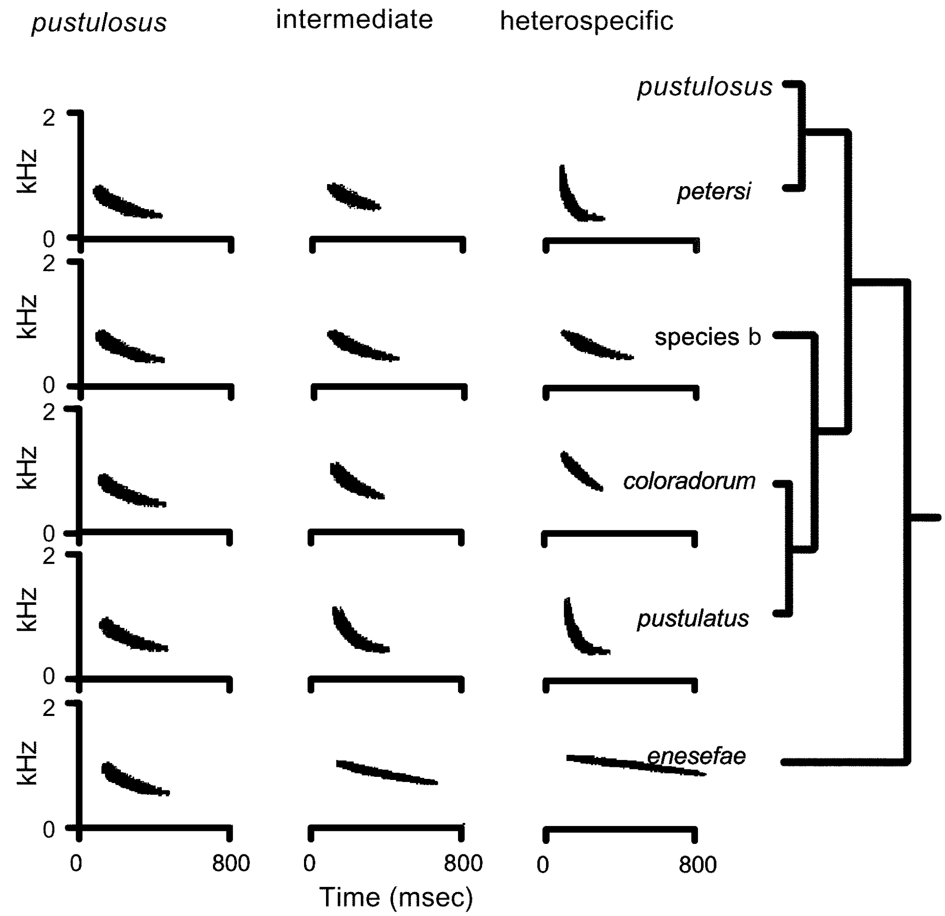

Figure 5: Sonograms of representative calls along each of the five call transects tested in this study. The transects are referred to by the heterospecific call that they contain. We illustrate calls at transect values of 0 (which is always the *Physalaemus pustulosus* call), 1 (which is always the heterospecific call), and 0.5 (which is one of the calls with values intermediate between the conspecific and heterospecific). The branching diagram illustrates the phylogenetic relationships among the species (Cannatella et al. 1998).

This expectation was compared to the actual responses with a Fisher's exact test.

We used multiple dimensional scaling (MDS) to represent the average call of each species in multivariate space (Wilkinson 2000). Multiple dimensional scaling is a class of techniques that uses proximities among objects to generate a geometric configuration of points such that the degree of similarity or dissimilarity among objects in the proximity measures is reflected in the spatial representation of the MDS map (Kruskal and Wish 1978). Initially, we standardized call variables of all species to z scores. We then determined the euclidean distances for all pairwise comparisons of species based on the transformed call variables. The euclidean distances were used in the dissimilarity matrix in the MDS of the calls. Since the distance measures along the two axes of the MDS plot are arbitrary, we defined the túngara frog call as having x and y coordinates of 0. The position of the intermediate and caricature calls within a transect in MDS space were interpolated or extrapolated based on the coordinates of that heterospecific call and conspecific call.

To estimate repeatability, we tested females with five calls from the *P. pustulatus* transect. These calls had transect values of 0, 0.250, 0.500, 0.750, and 1. We then estimated the female's threshold for recognition; that is, the point along this call transect at which she switches between response and no response. Thus, for a single set of these calls, the frog might have any one of six thresholds, which are represented by transect values between or just outside of the calls (i.e., −0.125, 0.125, 0.375, 0.625, 0.875, 1.125; fig. 2). We estimated the threshold by summing the "errors" made by the frog for each possible threshold value. By "errors" we mean the number of times that females exhibited phonotaxis that was not consistent with a specific

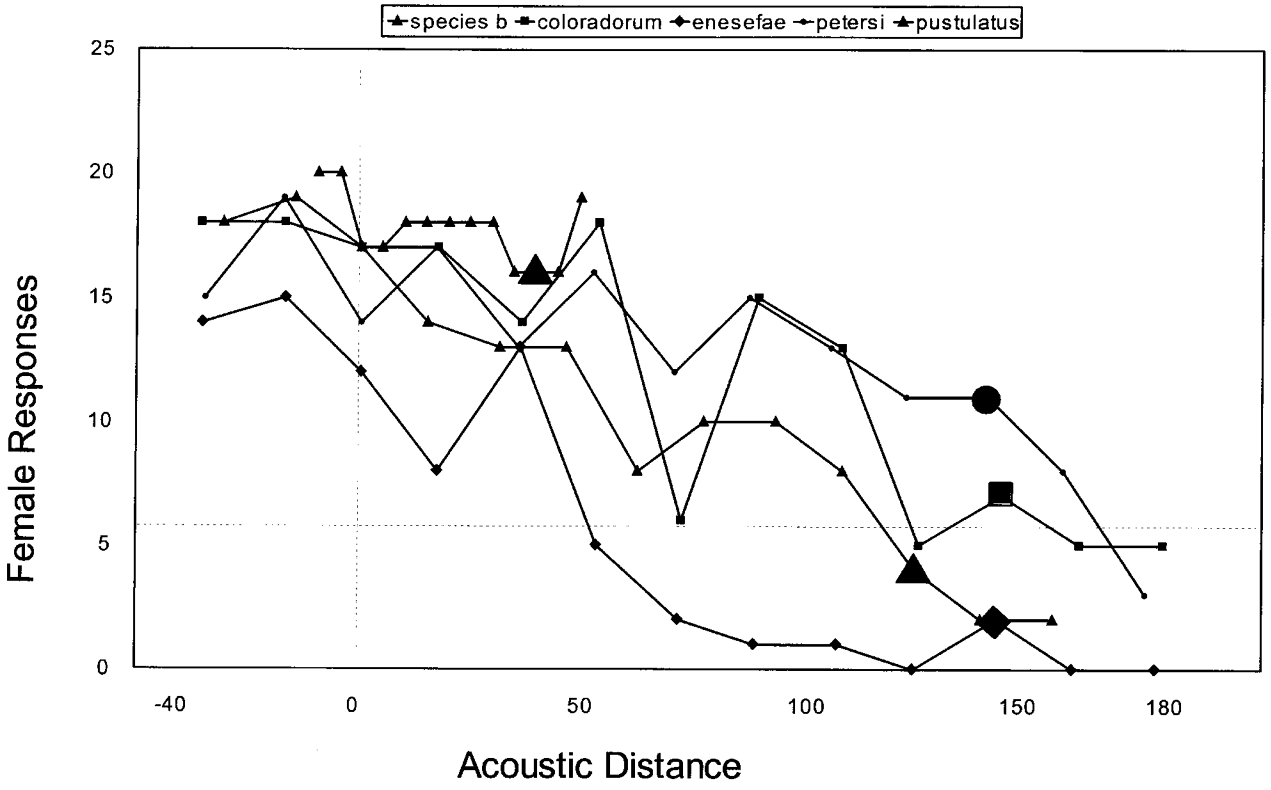

Figure 6: Number of responses from a sample of 20 females that elicited positive phonotaxis to calls along each of the five call transects studied. Acoustic distance is the euclidean distance between each call and the túngara frog call. The horizontal dashed line indicates the threshold for statistically significant recognition at $P < .05$. The vertical dashed line indicates the response to the conspecific call on each transect. The larger symbol within each transect represents the heterospecific call.

threshold value. For example, if the hypothesized threshold was 0.375, then phonotaxis toward stimuli 0.500, 0.750, or 1.00 (the heterospecific call) would be considered an error, as would lack of phonotaxis to stimuli 0 (the conspecific call) or 0.250. We then determined how well the frog's response in each trial fitted each threshold by summing these errors. We summed the errors in three ways: we simply summed the number of errors, we summed the errors weighting them linearly by how far they were from the proposed threshold, and we summed the errors weighting them quadratically by how far they were from the threshold. Our estimate of the "true" threshold was that threshold with the smallest summed error (or midway between two if there were two that fitted equally well).

We tested 10 females with this same transect of calls five times. This procedure gives five estimates of each of the 10 frogs' thresholds. We used a random effects, one-way ANOVA to test the null hypothesis that there were no significant differences among frogs in their thresholds.

We used logistic regression to compare the response of females to variation over a single transect. The euclidean distance of each call to the túngara frog call was the continuous independent variable, and the binary response of females was the dependent variable. There were 20 females tested in response to each of the 13 stimuli in a transect. Thus, in each regression analysis there were 260 binary responses equally partitioned among the 13 independent variables. Most females were tested with about one-fourth of the calls in a single transect, and they were not tested with calls in more than one transect. Therefore, the data are fairly independent among transects but not within transects. However, within a transect we are most interested in the general preference function and less interested in differences in responses between particular stimuli within the transect.

We used a randomization procedure to compare differences in logistic regression slope and intercept among transects. For each pair of transects compared, we randomly resorted each pair of call distance and female response values into two new randomized transect data sets. We calculated the absolute differences of logistic regression slope and intercept between the randomly resorted data

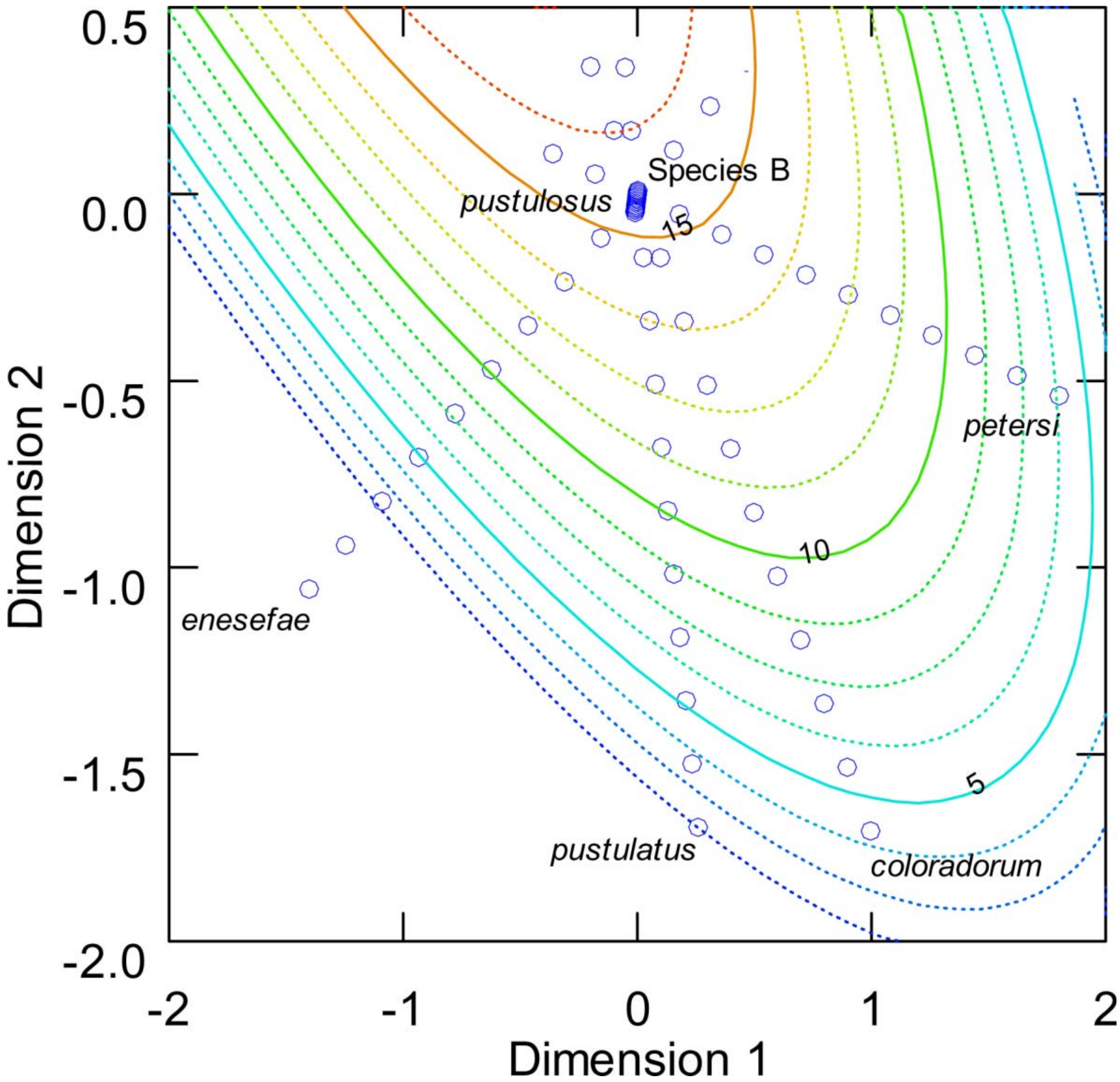

Figure 7: Calls along each of the transects are plotted in multidimensional scaling space, as in figure 3. The contours represent an estimated fit of the female phonotaxis data illustrated in figure 6 using a quadratic smoothing function (Wilkinson 2000). The numbers labeling the major contours represent the number of females from an $N = 20$ responding to the stimulus. Each transect is identified by the heterospecific call it contains. The coordinates of the *Physalaemus pustulosus* call are 0, 0. The first two dimensions of the multiple dimensional scaling explain 99% of the variation among call differences.

sets for each of 2,000 replicates per transect comparison. We then compared the absolute difference between the slope and intercept of the actual data to their distribution in the randomized data to determine the probability of the null hypothesis of no difference.

We used a paired *t*-test to compare the number of females responding to caricatures of the conspecific call to those responding to the noncaricature calls of the same acoustic distance from the conspecific call (e.g., the response to calls at positions -0.125 and -0.250 vs. 0.125 and 0.250; see fig. 2).

All analyses were conducted in SYSTAT 10 (Wilkinson 2000) with the exception of the logistic analysis, which was conducted in R (Ihaka and Gentleman 1996).

Results

The sample size for all experiments was 20. The null hypothesis of no recognition (18 no responses : 2 responses; Rand et al. 1992) was rejected if seven or more females responded to the test stimulus (Fisher's exact test, $P <$

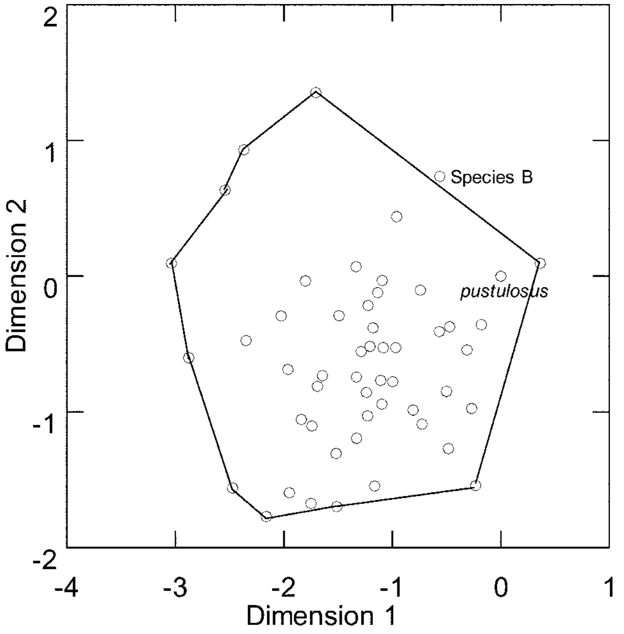

Figure 8: Plot of calls in multidimensional scaling space. The calls of *Physalaemus pustulosus* and Species B used in the study are plotted along with the calls of 50 males from the population where most of the females used in the study were collected. The first two dimensions of the multiple dimensional scaling explain 79% of the variation among call differences.

.05). Females showed statistically significant recognition in response to 49 of the 65 stimuli tested (fig. 6).

The degree of recognition of the heterospecific calls in this study was similar to our previous study of recognition of the same heterospecific calls (Ryan and Rand 1995): Species B, 16 recognition responses elicited from 20 females in this study (16/20) versus 10 of 20 (10/20) in the previous study; *Physalaemus coloradorum*, 7/20 versus 11/20; *Physalaemus enesefae*, 2/20 versus 0/20; *Physalaemus petersi*, 11/20 versus 4/20; and *Physalaemus pustulatus*, 4/20 versus 2/20 (fig. 5). The only qualitative difference between the studies is that the *P. petersi* call elicited statistically significant recognition in this study but not in the previous one.

The number of calls along each conspecific-heterospecific transect that elicited significant recognition varied substantially (figs. 6, 7). All of the calls along the Species B transect were recognized as conspecific. This heterospecific call, however, is much more similar to the conspecific call than are all the other heterospecific calls (fig. 3). The other heterospecific calls are more similar to one another in their acoustic distance from the conspecific call, yet there are still differences in the number of calls that elicited recognition along each transect. The number of recognized calls along the *P. coloradorum*, *P. pustulatus*, and *P. petersi* transect were 9, 10, and 12, respectively, while only five of the 13 calls along the *P. enesefae* transect yielded significant recognition.

The acoustic distance along the transect was a good predictor of the average number of females showing recognition to each stimulus. For all stimuli combined there was a strong correlation between female responses and call distance ($r = -0.79$, $P < .001$; figs. 6, 7). The same was true for all individual conspecific-heterospecific transects (*P. coloradorum*, $r = -0.85$; *P. enesefae*, $r = -0.90$; *P. petersi*, $r = -0.82$; *P. pustulatus*, $r = -0.97$; all, $P < .001$), with the exception of the Species B transect ($r = -0.52$, $P = .07$).

The strong recognition of calls on the Species B transect appears to result from the Species B call being so similar to the túngara frog call. Figure 8 shows a plot in MDS space of the mean call values of the *Physalaemus pustulosus* call and the Species B call in addition to the calls of 50 males from the populations that supplied most of the females we tested. (Note that the relationships among *P. pustulosus* and Species B differ between figs. 7 and 8 because the euclidean distances that provide the dissimilarity matrix for the MDS analysis are influenced by the group variance of the populations being compared, and the mean population *P. pustulosus* call in table 1 was calculated from a nearby population.) In this example, the *P. pustulosus* call we used lies just within the cloud of the 50 males from the test population. The Species B call we used falls just outside of this cloud. Thus, in the basic characteristics of the whine, *P. pustulosus* and Species B are quite similar and appear to be perceived by the females as such.

The pattern of female responses among transects tended to differ in both the slope and the intercept of the logistic regression (table 2). In the 10 pairwise comparisons of slopes among transects, seven comparisons showed statistically significant differences, and one showed a strong trend in that direction (*P. coloradorum* vs. *P. petersi*; $P = .07$). The two pairwise comparisons that appeared not to differ in slope were *P. coloradorum* versus *P. pustulatus* ($P = .53$) and Species B versus *P. petersi* ($P = .62$). *Physalaemus coloradorum* and *P. pustulatus* are sister species, the species within each of the two pairs are more similar to one another than to the other species in their call's acoustic distance, and the species within each pair have calls in similar regions of the acoustic landscape (figs. 3, 7). With a Bonferroni correction, in which the critical level of $P = .005$, an additional three of the above comparisons would not be statistically significant.

Six of the 10 pairwise comparisons among transects of the regression intercepts were significantly different, with the Species B versus *P. coloradorum* comparison showing a weak trend in that direction ($P = .12$; table 3). As in the slope comparison, *P. coloradorum* and *P. pustulatus* did

Table 2: Differences in slopes of the logistic regression (female response regressed on acoustic distance) between pairs of call transects

	Physalaemus coloradorum	*Physalaemus enesefae*	*Physalaemus petersi*	*Physalaemus pustulatus*
Species B	1.79, $P < .001$	3.38, $P < .001$	.90, $P = .620$	2.10, $P < .001$
P. coloradorum		1.58, $P = .006$	.89, $P = .070$	.31, $P = .530$
P. enesefae			2.47, $P < .001$	1.27, $P = .030$
P. petersi				1.20, $P = .013$

not differ from one another ($P = .41$), and they are closest relatives and closest to one another in both the magnitude and direction of call difference relative to the túngara frog. In addition, the intercept of the *P. petersi* transect did not differ from either of these two transects (vs. *P. coloradorum*, $P = .28$; vs. *P. pustulatus*, $P = .77$). With a Bonferroni correction, in which the critical level of $P = .005$, an additional two of the above comparisons would not be statistically significant.

The above comparisons of the shapes of the logistic regressions among transects show that not all points in acoustic space with the same acoustic distance from the túngara frog are perceived as equal by the females. This phenomenon was also exhibited in responses to stimuli that were or were not caricatures of the conspecific call but were the same absolute acoustic distance (fig. 2). For each transect, we compared the number of responses to the caricatures (the calls that differed from the conspecific by negative two-eighths [-0.250] and negative one-eighth [-0.125]) to calls of the same acoustic distance that were not caricatures (two-eighths [0.250] and one-eighth [0.125]; fig. 2). For example, in the Species B transect, female túngara frogs exhibited 20 responses to the -0.250 stimulus and 20 responses to the -0.125 stimulus but 18 responses to the 0.250 stimulus and 17 to the 0.125 stimulus. Females showed similar patterns of response to analogous stimuli on the other transects: *P. coloradorum* (18 and 18 vs. 14 and 18), *P. enesefae* (14 and 15 vs. 13 and eight), *P. petersi* (15 and 19 vs. 13 and 17), and *P. pustulatus* (18 and 19 vs. 13 and 14). There is a stronger overall response to the calls with negative call values (caricature) than to the calls with positive call values ($t = 3.639$, $\mathrm{df} = 9$, $P = .005$). For only the comparison of calls "close" to the conspecific call (i.e., ± 0.125), there is a trend toward greater response to the caricature calls ($t = 2.87$, $\mathrm{df} = 4$, $P = .094$) and a nearly significant bias to caricatures when comparing the "far" calls (i.e., ± 0.250; $t = 0.276$, $\mathrm{df} = 4$, $P = .051$).

When comparing the general pattern among transects, we find no evidence of a threshold or category effect (figs. 6, 7). Even though the pattern of response decrement often differs among transects, none of the transects suggests that the population is characterized by a threshold effect that defines calls as conspecific versus not conspecific. This impression was also borne out in studies of repeatability.

We compared the estimates of a female's threshold in the five repeated trials (fig. 9). The ANOVAs revealed significant difference among females in their thresholds as estimated by all three models: the unweighted error model ($F = 4.08$, $\mathrm{df} = 9, 40$, $P < .001$), the linearly weighted model ($F = 4.10$, $\mathrm{df} = 9, 40$, $P < .001$), and the quadratically weighted model ($F = 3.78$, $\mathrm{df} = 9, 40$, $P = .002$). Within frogs, however, there was very little consistency in their thresholds; they ranged from 0.125 to 0.85 (averaging 0.5), and their coefficients of variation ranged from 6% to 140% (averaging >50%; linear model). We reject a mechanistic model "fixed threshold" for the species or even for individual frogs in favor of a probabilistic model in which there might be a large number of covariates internal and external to the frog.

Discussion

We addressed several questions in this study. Do stimuli that differ from the conspecific call elicit recognition from female túngara frogs? Does acoustic distance from the test call to the conspecific call predict female response? Do the patterns of response suggest that females form categories of conspecific and heterospecific (Ehret 1987), or do they exhibit more continuous variation in their response (Shepard 1987)? Does the shape of the preference function vary as a function of the acoustic landscape? Do females show enhanced response to caricatures of conspecific calls (Enquist and Arak 1998)? Are there repeatable differences among females in their threshold for recognition?

This study aptly documents the general result of false recognition that we have shown elsewhere: a large number of acoustic stimuli elicit recognition from females. We believe such apparent permissiveness in signal recognition results from a lack of selection on the response to allopatric-heterospecific signals combined with a process analogous to if not homologous with the psychological process of generalization. The túngara frog's mating call is species specific, but this does not mean that it is invariant; "species specific" instead means that the variation among mating call characteristics within the species is less than the var-

Table 3: Differences in intercepts of the logistic regression (female response regressed on acoustic distance) between pairs of call transects

	Physalaemus coloradorum	*Physalaemus enesefae*	*Physalaemus petersi*	*Physalaemus pustulatus*
Species B	.61, $P = .120$	1.94, $P < .001$	1.01, $P = .010$	.90, $P = .013$
P. coloradorum		1.33, $P < .001$	.40, $P = .280$	.29, $P = .410$
P. enesefae			.93, $P < .001$	1.04, $P = .002$
P. petersi				.11, $P = .770$

iation among species (also see Barlow 1977 on fixed vs. modal action patterns). Thus, all animals are faced with the problem of recognizing a signal that indicates an appropriate, usually conspecific, mate over a certain range of variation. One way to understand how these recognition decisions are made is to examine the preference function (Ritchie 1996; Wagner 1998; Gerhardt et al. 2000) or generalization gradient (Shepard 1987) of recognition as a function of stimulus variation.

The acoustic distance from the conspecific call to the test call predicted the response of females. The probability of females responding to test stimuli decreased as the acoustic distance between the conspecific and test stimuli increased. Similar results have been shown in other frogs in response to variation in single call parameters (reviewed in Gerhardt 2001; Gerhardt and Huber 2002). With the exception of the Species B transect (whose heterospecific call is quite similar to the conspecific call; fig. 8), the frogs respond to stimulus variation within each transect in a quite predictable manner: acoustic distance predicts between 67% and 94% of the variation in female responses. We suggest that the female frogs are generalizing (Shepard 1987). An alternative explanation is that females falsely recognize some test stimuli because their auditory systems cannot perceive the difference between those stimuli and the conspecific call. This is not the case, however. When falsely recognized calls are presented to females along with a conspecific call in a discrimination test, there is almost always a strong preference for the conspecific call (Ryan and Rand 1995, 1999, 2001). Thus, the females can perceive a difference between conspecific and other calls but will often respond to a nonconspecific call in the absence of the conspecific call.

Given that the probability of response to stimuli varies continuously with acoustic distance, it is not surprising that our data also show no evidence that these animals are forming categories of conspecific versus the other stimuli that we tested. If there were categorical perception, each of the transects that span high to low responsiveness should approximate a step function rather than a linear one. Inspection of figure 6 suggests this is not the case. Furthermore, females would not show preferences for conspecific calls over other calls that elicit recognition when broadcast in isolation if perception were categorical. In addition, the repeatability tests show that even individual females do not have highly predictable thresholds in discerning between conspecific and heterospecific calls. Thus, the population's pattern of gradual decrement in response to increasing stimulus difference seems to reflect the similar probabilities of individual females responding to a stimulus rather than a polymorphism in categorical responses by females. We have reached a similar conclusion in another study of repeatability in túngara frogs to different suites of stimuli (Kime et al. 1998).

Our results, therefore, do not support the predictions of categorical perception in frogs made by Ehret (1987). He suggested that frogs should continuously perceive variation in male aggressive signals but categorically perceive variation in mate recognition signals. His suggestion was based on the assumption that useful information is encoded in the continuous variation in aggressive calls but that only species identity is encoded in the mating call; any variation in the conspecific signal is probably meaningless. We know, however, that this need not be the case, as many frogs (e.g., Welch et al. 1998; Wollerman 1998; Giacomo and Castellano 2001; Marquez and Bosch 2001), including túngara frogs (e.g., Ryan 1980; Ryan and Rand 1993*a*), are quite attendant to such variation. We do not know if frogs are capable of categorical perception, but other studies of frogs have failed to show this ability (Gerhardt 1978, 2001). Chinchillas (Kulh and Miller 1975) and quail (Kluender et al. 1987) respond categorically to human phoneme variation, and some birds (Nelson and Marler 1989) and insects (Wyttenbach and Hoy 1999) categorically perceive more biologically relevant stimuli, but our data show that túngara frogs do not do so in response to these stimuli. It is possible that frogs might show categorical perception in other contexts. For example, Wyttenbach and Hoy (1999) have shown that crickets exhibit categorical discrimination between stimuli that mimic the conspecific mating call and a bat echolocation signal. These signals are quite different from one another, and the cost of false recognition could be more detrimental than a heterospecific mating. An analogous situation might be to test for categorical discrimination between mating calls

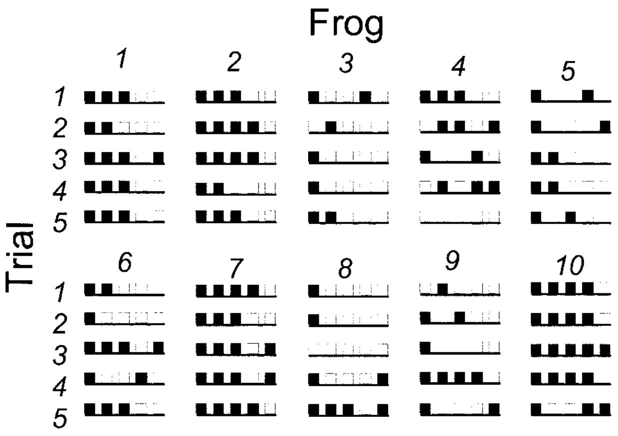

Figure 9: Each of the 10 blocks of data illustrates the response of each of 10 females in the repeatability tests. The five columns in each block represent the five calls along the call transect used in the repeatability studies. A closed box indicates that the female showed positive phonotaxis to a stimulus, and an open box indicates that it did not. Each female was tested to the same five calls five times, as indicated by the rows within each set of data. The stimuli more similar to the conspecific call are on the left, and those more similar to the heterospecific call are on the right. Specifically, from left to right call values are 0, 0.250, 0.500, 0.750, and 1.

and fire sounds in frogs that are known to flee from the latter (Grafe et al. 2002).

Given that the acoustic distance from the conspecific call is a good, general predictor of female recognition and that the probability of response changes continuously rather than categorically, we asked if this pattern of covariation of stimulus and response—that is, the shape of the preference function—varies across the acoustic landscape. We are interested in this result because an animal's more recent ancestors will have calls in certain parts of the acoustic landscape. If the brain's past history influences how it functions, as we have argued elsewhere (Ryan et al. 2001), then we predict that the shape of preference functions should vary over the acoustic landscape. We have reached this conclusion in other studies of túngara frogs in which we combined phonotaxis data from female túngara frogs with artificial neural networks simulations. In those studies we showed that the past history of mating calls that needed to be recognized by ancestors influences how the túngara frog recognizes calls today (Phelps and Ryan 1998, 2000; Phelps et al. 2001).

There are two suggestions of an effect of history in this study. First, although all the transects but Species B are quite predictable in their relation between stimulus variation and female response, they are not invariant. The slopes and intercepts of the logistic regressions often differ among transects. Furthermore, in comparisons of caricature to noncaricature calls of the same acoustic distance from the conspecific call, the caricature calls elicit greater recognition (figs. 2, 6). We cannot posit the same explanation that Enquist and Arak (1998) offered to explain why humans often mistakenly identify a caricature drawing of a human face as the more accurate rendition of that face. They argued that humans tend to concentrate on characters that are diagnostic and suggested the same might be true in animal species recognition. In this case, however, we are comparing allopatric species so that such recognition problems are not an issue. Thus, the data on response to caricatures show that stimuli of the same acoustic distance from the conspecific call are not all perceived as equal by the females, although in this case we are not sure why this is so. One possibility is that the caricature suggests to females a mate of high quality (Andersson 1994), although nothing about the biology of túngara frogs suggests this.

Despite a near universal preference for conspecific signals over heterospecific ones in the animal world, we show that in many cases, at least with signals of allopatric species, female túngara frogs falsely recognize many signals as being conspecific. Furthermore, females do not perceive such stimulus variation categorically, but the probability of responding varies continuously with attributes of the stimulus. Furthermore, we suggest that the past history of the species might explain why the relationship between stimuli and response varies across the acoustic landscape.

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