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ORIGINAL ARTICLE

Lori Wollerman · R. Haven Wiley

Possibilities for error during communication by neotropical frogs in a complex acoustic environment

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Abstract Differences in vocalizations promote accurate identification of species during mate choice. The properties of vocalizations vary, however, and overlap in the properties of different species' calls raises the possibility of errors in species identification. A general model of these possibilities is provided by discriminant function analysis (DFA). To illustrate this use of DFA, we consider possibilities for error in the classification of advertisement calls by *Hyla ebraccata* in a diverse community of neotropical hylid frogs. The analysis used three features of their calls: duration, dominant frequency, and pulse repetition rate, separately and in combination. These properties are known to be used for mate choice by female *H. ebraccata* and many other species of frogs. With only one feature, DFA misidentified 12–32% of individuals, either by assigning *H. ebraccata* calls to other species (missed detections) or by assigning calls of other species to *H. ebraccata* (false alarms). With two call parameters, DFA committed few or no errors. If the analysis included the relative abundances of the different species, there were even fewer errors. Thus DFA can use as few as two features to identify calls of *H. ebraccata* almost without error. The dispersion of the different species in discriminant-function space was random, not overdispersed as expected, regardless of the call features included in the analysis. The lack of overdispersion might be explained by differences in selection on calls of common and rare species. This application of DFA indicates several ways in which understanding the possibilities for errors can advance our understanding of the evolution of communication in general.

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L. Wollerman (✉) · R.H. Wiley
Department of Biology, University of North Carolina,
Chapel Hill, NC 27599–3280, USA
e-mail: lwollerman@hood.edu
Tel.: +1-301-6963648, Fax: +1-301-6963667

L. Wollerman
Department of Biology, Hood College, 401 Rosemont Avenue,
Frederick, MD 21701–8575, USA

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Introduction

Female frogs of many species choose mates, at least in part, by recognizing the species-specific calls of males (reviewed by Gerhardt 1994a, b). For accurate recognition, each species' calls must differ from those of other species. The advertisement calls of species breeding at the same time and place usually differ significantly in the mean values of their acoustic properties (Fouquette 1960; Duellman 1967; Hödl 1977; Drewry and Rand 1983; Duellman and Pyles 1983; Schwartz and Wells 1984). Nevertheless, even when the means differ, the distributions of the properties of different species' calls often overlap (Fouquette 1960; Littlejohn 1977; Duellman and Pyles 1983; Schwartz and Wells 1984; Littlejohn et al. 1985). This situation could lead to errors in recognition of conspecifics.

The possibility of error during mate choice by frogs exemplifies a general feature of all communication. Errors can occur whenever decisions to act are based on recognition of signals that are not absolutely distinct to the receiver (Wiley 1994). In this paper, we examine overlap in the properties of calls of different species of frogs to determine the possibility of error in species recognition and the degree to which combinations of properties of calls could reduce this possibility.

In the Atlantic lowlands of Costa Rica, females of the treefrog *Hyla ebraccata* search for mates in multispecies choruses. A female searching for an appropriate mate must make decisions about which calls evoke responses. Regardless of the mechanism for her decision, she inevitably faces four possible outcomes every time she makes a decision to respond or not (Wiley 1994). If a female accepts a call as a potential mate's, her response is either a correct detection (if the call is in fact a conspecific's) or a false alarm (if it is not). If she rejects a signal, her response is either a correct rejection (if the call is not a conspecific's) or a missed detection (if it is). Missed detections and false alarms are errors in the sense that they incur additional costs for a female, for example more time searching for a mate or increased risks of mismating. Similar possibilities for error recur in all forms of communication.

The four possible outcomes of any decision by a receiver to respond to sensory stimulation have analogs in discriminant function analysis (DFA). This procedure calculates a set of functions that maximally separate categories of objects specified by multiple parameters. The discriminant functions, linear combinations of these parameters, define axes that provide the greatest differentiation among these objects. They also determine the relative frequencies of each kind of error. An object belonging in a target category but incorrectly included in another category is a missed detection; an object belonging in another category but incorrectly included in the target category is a false alarm.

Although DFA can help to understand some possible constraints on mate choice, we do not propose that it is a realistic model for the actual mechanism of mate choice by a female frog. First, we might not yet be aware of all of the parameters important for mate choice by any frog. Nevertheless, studies of a variety of species have identified some of these parameters. Second, it is unlikely that the neural mechanisms for making decisions to respond to stimulation are accurately represented by linear combinations of parameters. This limitation of DFA is not so severe as might be imagined, because multiple linear functions can approximate more complex functions. For instance, two linear functions with respectively negative and positive coefficients of the same parameter could describe a class of objects from others with higher and lower values for this parameter, much as a tuning curve would do. Finally, a female frog does not face the problem of distinguishing calls of all the species she hears. She only has to distinguish the calls of her own species from all others. Female frogs might thus evolve more efficient means to accomplish this more limited task. In sum, linear DFA is a conservative model for minimizing error in communication. We expect that female frogs would do at least as well.

In this study we focused on recognition of the advertisement calls of *H. ebraccata* in the Caribbean lowlands of Costa Rica. We constructed discriminant functions for classifying calls of six syntopic species based on three parameters of males' advertising calls, all known to affect mate choice by *H. ebraccata* (Wells and Bard 1986; Wollerman 1998). We then used these discriminant functions to assess the frequency and nature of errors in attempting to recognize calls of *H. ebraccata*. We also considered the possibility that different species' calls would evolve to minimize overlap with those of their "nearest neighbors" in acoustic space, so that species' calls would become overdispersed in acoustic space.

Methods

Study site

We studied hylid frogs from 1991 to 1993 at La Selva Biological Station, Costa Rica, in Atlantic lowland rainforest. Vegetation at the site, a seasonally flooded marsh at 250 m N on Camino Experimental Sur, included *Spathiphyllum friedrichsthalii* (Araceae) and *Panicum grande* (Poaceae)(Donnelly and Guyer 1994). In addition to *Hyla ebraccata*, 12 species of frogs called here during this study: *Agalychnis callidryas*, *Agalychnis saltator*, *Scinax boulengeri*, *Scinax elaeochroa*, *Hyla phlebodes*, *Hyla loquax*, *Hyla rufitela*, *Smilisca baudinii* (Hylidae); *Eleutherodactylus diastema*, *Leptodactylus pentadactylus* (Leptodactylidae); *Gastrophryne pictiventris* (Microhylidae); and *Rana vallianti* (Ranidae).

Advertisement calls

Advertisement calls were recorded with a Sony TC-D5M (1991 and 1992) or a Marantz PMD 221 (1993) tape recorder and a Sennheiser K3U/ME80 microphone. Air temperature at the site during these field seasons varied from 22.5°C to 25.0°C. After we had recorded its calls, each frog was captured, weighed to the nearest 0.05 g, measured (snout–vent length) to the nearest 0.1 mm, toe-clipped for identification, and then released. We recorded individuals of six species of hylid frogs (*Hyla ebraccata*, *H. loquax*, *H. phlebodes*, *Scinax boulengeri*, *S. elaeochroa*, *Smilisca baudinii*). *Agalychnis saltator*, *A. callidryas* and *E. diastema* called from high in trees (3–20 m); because they were spatially separated from other species they were not included in this analysis. Of the remaining species not included in the analysis, three (*H. rufitela*, *G. pictiventris*, and *R. vallianti*) rarely called at the study site and most of the calling by *L. pentadactylus* was earlier in the season than that of any of the other species.

We measured dominant frequency, call duration, and pulse repetition rate of calls with a Uniscan real-time spectrum analyzer interfaced to a 68000 microcomputer or with Avisoft software on a 586 microcomputer with a ProAudio 16-bit D-to-A converter. We included only the primary note in analyses for *H. ebraccata* and *H. phlebodes*, species that sometimes add a secondary note to their call. Two or three calls (from the beginning, middle, and end of recordings of individual males) were measured for each male and the average of these calls used in the subsequent analyses. Calls were digitized with a sampling rate of 10 kHz. Spectral measurements had a precision of 80 Hz, temporal measurements a precision of 12.5 ms. We calculated the population mean, standard deviation, and within-male coefficient of variation of each parameter of calls for each species. We did not correct any call properties for the effect of temperature because variation in temperature was slight.

Discriminant function analysis

To separate advertisement calls of *H. ebraccata* from those of other species, we used DFA as implemented in SYSTAT (Wilkinson 1989). This process computes linear combinations of variables that maximally separate groups by maximizing the ratio of between-group to within-group variance (Dillon and Goldstein 1984; Wilkinson 1989). In separate analyses, we used each of the three call properties (call duration, dominant frequency, and pulse repetition rate) alone, in pairwise combinations, and in a three-way combination. We selected these call properties because in two-speaker playback experiments females discriminate calls that differ in these characteristics (Wells and Bard 1986; Wollerman 1998). Using the equations generated by the DFA, we could then check the accuracy of the assignments of individuals to groups. For calls of *H. ebraccata*, we compared the actual group membership of calls with the predicted group membership for each combination of call properties. We did not split the calls into two sets,

Table 1 Properties of advertisement calls of six species of treefrogs: means ± standard deviations; *CV* means of within-male coefficients of variation; *n* number of individuals. Data for *Hyla ebraccata* are from Wollerman (1998)

Species	*n*	Dominant frequency (Hz)	Call duration (s)	Pulse repetition rate (Hz)
Hyla ebraccata	57	3,262.9±146.8	0.162±0.017	96.2±4.2
CV	60	1.1%	2.1%	6.8%
H. loquax	16	2,946.7±114.0	0.070±0.011	101.5±8.8
CV	22	1.8%	4.3%	5.0%[a]
H. phlebodes	12	3,824.6±215.3	0.062±0.012	162.0±5.2
CV	12	0.9%	2.2%	10.8%
Scinax boulengeri	7	2,891.7±230.6	0.303±0.048	248.5±34.9
CV	7	3.1%	4.8%	16.9%
S. elaeochroa	22	3,370.5±114.6	0.220±0.060	45.6±1.7
CV	24	0.8%	1.6%	10.6%
Smilisca baudinii	5	2,315.3±114.9	0.086±0.018	177.8±17.5
CV	5	1.2%	1.9%	7.9%

[a] *n*=10

Table 2 Statistical analysis of differences in the calls of species based on one parameter

Analyses of variance (ANOVA) with single properties			
Call parameter	*df*	*F*	*P*
Pulse repetition rate	5	697.4	<0.001
Call duration	5	94.3	<0.001
Dominant frequency	5	94.3	<0.001

one for DFA and the other for assignments, because our objective was to examine the accuracy of a DFA when provided the greatest amount of information rather than to evaluate its classification of unknown signals.

In any DFA, the probability of including individuals in a particular group depends on the relative abundance of that group. So we repeated the DFA of frogs' calls with approximately natural relative abundances of the species: 0.47 for *H. ebraccata*, 0.14 for *H. loquax*, 0.09 for *H. phlebodes*, 0.06 for *Scinax boulengeri*, 0.19 for *Scinax elaeochroa*, and 0.05 for *Smilisca baudinii*. These probabilities are the proportions of calls from each species in our recordings and roughly match the species' relative abundances in the field estimated from surveys of calling frogs.

If selection has acted to maximize the distinctiveness of species' calls, then the calls of different species should be overdispersed, rather than randomly distributed, in discriminant function space. To test this hypothesis, we calculated nearest-neighbor distances (Clark-Evans tests, Clark and Evans 1954) for population means of calls with Campbell software (Krebs 1989). 'Neighbors', in this case, were species located in acoustic space as defined by the discriminant function.

Results

There was significant variation among the six species in each of the three call properties separately and for all possible combinations of the properties (Tables 1, 2, 3, 4, Fig. 1). Females could thus use any of these acoustic properties to identify the correct species with which to mate.

Nevertheless, properties of the calls of different species often overlapped. The DFAs calculated linear functions that optimally differentiated the calls of the six species. In all but one DFA (the one based on dominant frequency and call duration), each canonical factor was highly correlated with one call parameter (Table 5). When pulse repetition rate was included in the analysis, it always had the highest loading on the first canonical factor.

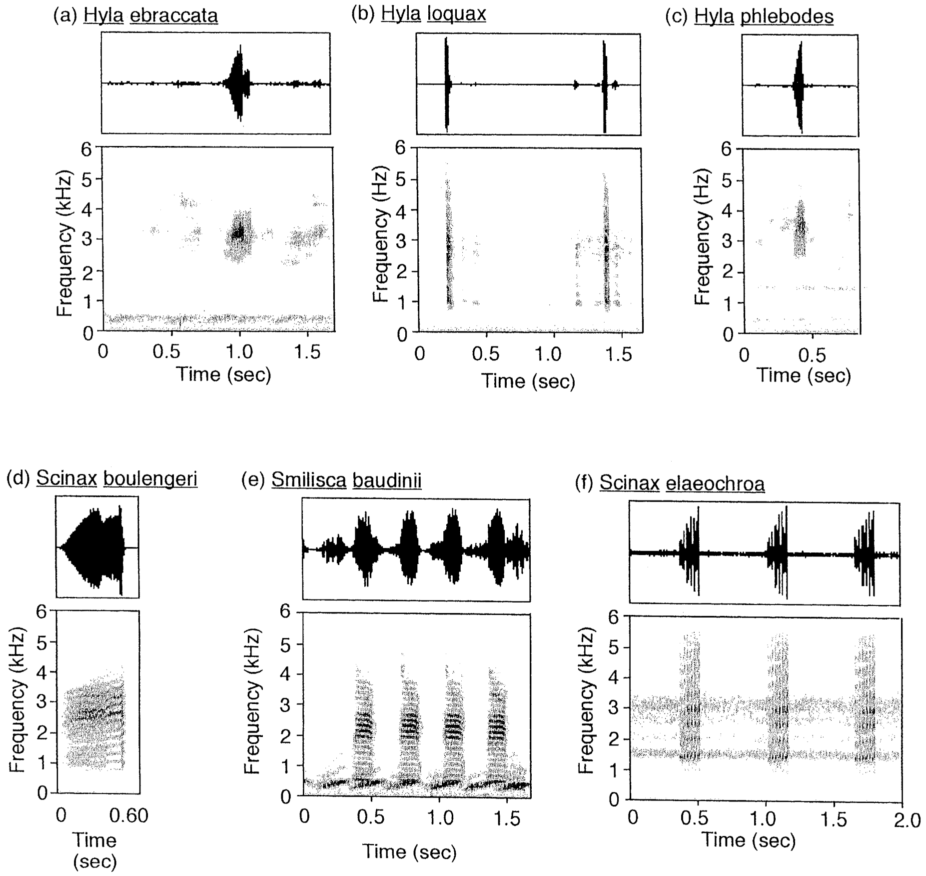
Using these DFAs, we calculated the number of correct and incorrect classifications of *Hyla ebraccata* calls based on different combinations of acoustic properties. Misclassifications were either false alarms (categorizing an individual as *H. ebraccata* when it was not) or missed detections (categorizing *H. ebraccata* as a different species). The ratio of these misclassifications to the total number of classifications indicated the overall reliability of classification. This procedure indicated how accurately calls of *H. ebraccata* were identified by each of these linear combinations of properties.

Table 3 Statistical analysis of differences in the calls of species based on two parameters. *T2* Hotelling-Lawley trace statistic

ANOVA with pairs of properties							
Call parameter	Univariate statistics			Multivariate statistics			
	df	*F*	*P*	*df*	*T2*	*F*	*P*
Dominant frequency	5	94.3	<0.001	10, 236	32.0	378.0	<0.001
Pulse repetition rate	5	671.5	<0.001				
Dominant frequency	5	99.2	<0.001	10, 224	8.9	100.0	<0.001
Call duration	5	102.8	<0.001				
Pulse repetition rate	5	667.4	<0.001	10, 228	36.1	411.5	<0.001
Call duration	5	94.3	<0.001				

Table 4 Statistical analysis of differences in the calls of species based on three parameters. *T2* Hotelling-Lawley trace statistic

ANOVA with all three properties							
Call parameter	Univariate statistics			Multivariate statistics			
	df	*F*	*P*	*df*	*T2*	*F*	*P*
Dominant frequency	5	99.2	<0.001	15, 332	40.9	301.6	<0.001
Pulse repetition rate	5	641.9	<0.001				
Call duration	5	102.8	<0.001				



(a) Hyla ebraccata (b) Hyla loquax (c) Hyla phlebodes (d) Scinax boulengeri (e) Smilisca baudinii (f) Scinax elaeochroa

Fig. 1a–f Oscillograms (*above*) and spectrograms (*below*) of advertisement calls of species used in this study. In **e**, the low frequency-modulated calls are *Leptodactylus pentadactylus*

With only one acoustic property DFA could not identify all conspecific males correctly (Fig. 2a). Duration of calls led to fewer errors (12%) than either pulse repetition rate (20%) or dominant frequency (32%). Combinations of two acoustic properties produced fewer errors (dominant frequency and pulse repetition rate, dominant frequency and call duration) or none (duration and pulse repetition rate) (Fig. 2a). A combination of all three variables could not improve discrimination further; in fact, adding dominant frequency to the latter combination of two properties introduced confusion and resulted in one error (Fig. 2a). Calls of *H. ebraccata* were confused most often with those of *H. loquax* or *Scinax elaeochroa*; each accounted for 47% of the total number of errors. Most of these errors were missed detections rather than false alarms (Fig. 2b).

Table 5 Loadings of call properties on canonical functions (factors) in the discriminant function analysis

Parameter	Dependent canonical function		
	1	2	3
Two-parameter analyses			
Dominant frequency	–0.64	0.77	
Call duration	0.74	0.68	
Dominant frequency	–0.12	0.99	
Pulse repetition rate	0.99	0.14	
Pulse repetition rate	0.94	–0.35	
Call duration	0.36	1.00	
Three-parameter analyses			
Dominant frequency	–0.13	0.42	0.90
Call duration	0.06	–0.88	0.48
Pulse repetition rate	0.92	0.40	–0.02

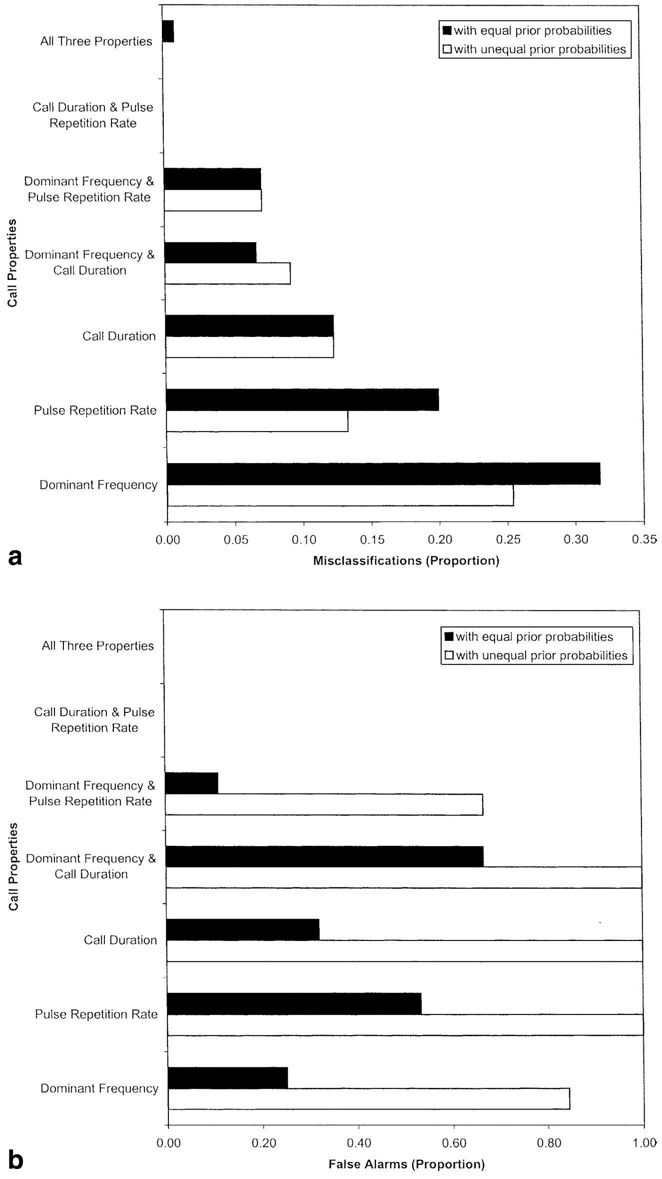
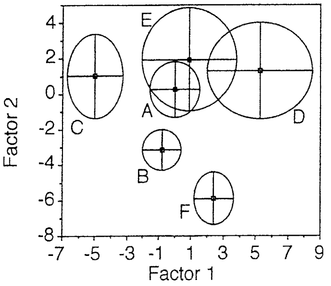


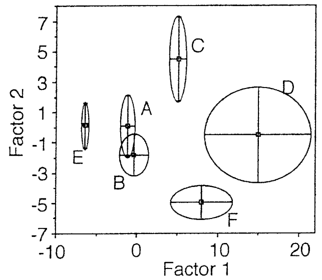
Fig. 2 **a** Misclassifications, expressed as a proportion of total assignments, of advertisement calls of *Hyla ebraccata* with discriminant function analysis. **b** Proportion of misclassifications that were false alarms

In general, unequal prior probabilities improved classification of *H. ebraccata* calls. If only one acoustic parameter was used to classify individuals, error rates with call duration (12%) and pulse repetition rate (13%) were lower than with dominant frequency (25%). Combinations of two or more variables decreased errors substantially (Fig. 2a). No errors were made with call duration and pulse repetition rate or with all three variables. As before, calls of *H. ebraccata* were most often confused with those of *H. loquax* (41% of all errors) and *S. elaeochroa* (52% of all errors). In contrast to classification with equal probabilities of group membership, most of the errors in this analysis were false alarms rather than missed detections (Fig. 2b).

(a) Dominant frequency and call duration



(b) Dominant frequency and pulse repetition rate



(c) Call duration and pulse repetition rate

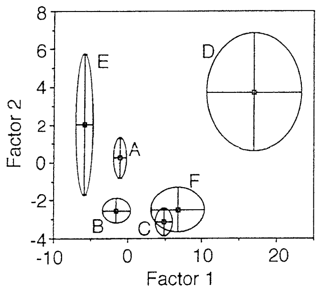


Fig. 3a–c Distributions of six species' calls in discriminant function space when discriminant functions incorporated two call properties. **a** Dominant frequency and call duration; **b** dominant frequency and pulse repetition rate; **c** pulse repetition rate and call duration. See Table 5 for loadings of call properties on canonical functions. The ellipses are centered on the population means; *bars* indicate 2 SD. A *Hyla ebraccata*, B *H. loquax*, C *H. phlebodes*, D *Scinax boulengeri*, E *S. elaeochroa*, and F *Smilisca baudinii*

The locations of the species' means in discriminant-function space did not differ significantly from random for any combination of acoustic properties (*R*=0.96–1.4, NS). However, across all four DFAs, there was a consistent pattern of overdispersion of calls (*R*>1), rather than aggregation (*R*<1) (Figs. 3, 4).

Discussion

In our DFAs, classification of calls based on single properties of calls inevitably led to errors in discrimination of calls of *Hyla ebraccata* from those of syntopic species. Combinations of two properties improved discrimination, yet more than two parameters did not further improve accuracy. In addition, the distribution of the species' calls in signal space defined by the canonical functions did not differ significantly from random, despite a consistent

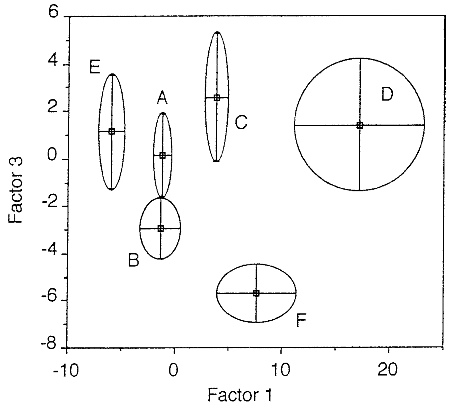


Fig. 4 Distributions of six species' calls in discriminant function space when discriminant functions incorporated three call properties: dominant frequency, call duration, and pulse repetition rate. See Table 5 for loadings of call properties on canonical functions. The ellipses are centered on the population means; *bars* indicate 2 SD. A *Hyla ebraccata*, B *H. loquax*, C *H. phlebodes*, D *Scinax boulengeri*, E *S. elaeochroa*, and F *Smilisca baudinii*

trend toward overdispersion. In the following sections we first consider the application of DFA to our samples of calls in this particular case. We then consider DFA as a model for errors in communication in general and, finally, the consequences of unequal abundances of species on the evolutionary divergence of calls in signal space.

DFA: application to frogs at La Selva

The advertisement calls of the six species considered in this study differed significantly from each other. These results are thus similar to those of Schwartz and Wells (1984), who showed the same patterns in a DFA of the calls of *H. ebraccata*, *H. microcephala*, and *H. phlebodes* from Panama. Despite the significant differences, there was overlap between species in each call property (Tables 1, 2, 3, 4, Figs. 3, 4). Whenever overlap occurred in the distributions of one or more properties, DFA misclassified some calls of *H. ebraccata*. For example, the combination of dominant frequency and pulse repetition rate resulted in errors in classifying calls of *H. ebraccata*, as expected from the overlap between *H. ebraccata* and *H. loquax* in discriminant function space (Fig. 3b).

If female *H. ebraccata* were to use only one parameter to classify conspecific calls, the DFA indicated that the most reliable was the duration of the primary note. If females also considered the prior probability of a conspecific signal (a correlate of the species' relative abundance), they could do equally well with either call duration or pulse repetition rate alone. The dominant frequency was the least accurate predictor of species identity, regardless of whether or not the DFA considered the relative abundance of different species. Dominant frequency was also a poor predictor of species identity in other neotropical frogs (Duellman and Pyles 1983; Schwartz 1987a), but fundamental frequency (a property not included in this study) was the best predictor of species identity in a DFA of Guyanan treefrogs (Bourne and York 2001).

DFA does not require parameters that are independent of each other (Dillon and Goldstein 1984; Wilkinson 1989). However, it does require parameters with homogeneous variance-covariance matrices. In our study, there were a few probable violations of this assumption of homoscedasticity. The variance of pulse repetition rate of *Scinax boulengeri* was larger than for the other species (Table 1). In addition, call duration and pulse repetition rate covaried in *H. ebraccata* and *S. elaeochroa* (Table 6). As a consequence, the calculated canonical functions were probably not the best linear unbiased estimators, and the statistical tests were conservative (Dillon and Goldstein 1984). Inspection of the residuals of the analyses of variance indicated that several outliers existed. When analyses were repeated with outliers removed, the results showed that the initial tests were in fact conservative.

The parameters of calls that we included in our analyses are not the only possibilities. For many species, the properties of conspecific calls that influence mate choice remain poorly known. For instance, advertisement calls of *H. microcephala*, *H. phlebodes*, and *H. ebraccata* differ in the rise time of pulses (Schwartz and Wells 1984), a property known to affect females' responses in *Hyla versicolor* (Gerhardt and Doherty 1988) but so far not investigated in these Central American species.

Even though our analysis did not include all possible call properties, it included ones that often affect female frogs' choices. In two-speaker playback experiments, females of a variety of species, including *H. ebraccata* (Wells and Schwartz 1984; Wells and Bard 1986), prefer

Table 6 Pearson's correlation coefficients between call properties used in discriminant function analyses. Significance tests employed the Bonferroni correction for multiple tests

Species	*n*	Frequency and pulse repetition rate		Frequency and call duration		Call duration and pulse repetition rate	
		r	*P*	*r*	*P*	*r*	*P*
Hyla ebraccata	57	–0.01	1.0	–0.03	1.0	–0.41	<0.01*
H. phlebodes	12	0.11	1.0	0.48	0.36	–0.14	1.0
H. loquax	16	–0.22	1.0	–0.13	1.0	–0.15	1.0
Scinax boulengeri	8	0.32	1.0	–0.12	1.0	–0.61	0.32
S. elaeochroa	22	–0.21	1.0	0.20	1.0	–0.63	<0.01*
Smilisca baudinii	5	–0.89	0.14	0.24	1.0	–0.57	0.94

* Statistical significance

conspecific calls with longer duration (Gerhardt 1994b). Female *H. ebraccata* (Wollerman 1998) and other species (Gerhardt 1994b) also prefer calls of lower dominant frequency. Females of some species prefer calls of species-typical dominant frequency (Gerhardt 1994b), and females of most species, including *H. ebraccata* (Wollerman 1998), generally prefer the species-typical pulse repetition rate (Gerhardt 1994b).

Females' responses to properties of calls can fit either monotonic or unimodal functions. For instance, responses to call duration and dominant frequency are usually monotonic, if not linear, functions of these features (Wells and Schwartz 1984; Wells and Bard 1986; Wollerman 1998). Such responses produce directional selection. On the other hand, responses to features that are important for species discrimination, such as pulse repetition rate, are often unimodal rather than monotonic functions of these properties (Wollerman 1998) and thus produce stabilizing selection (Gerhardt 1991, 1994b). Unimodal or tuned responses recur throughout the auditory processing of sound in vertebrates. The basilar papilla of *H. ebraccata*, for instance, has a tuning curve that is maximally sensitive at 2,077 Hz (McClelland et al. 1997).

Both unimodal and monotonic response functions can be approximated by the multiple discriminant functions of a DFA, but it is not yet possible to compare multidimensional discriminant functions with the actual behavior of female frogs. It would take a large experimental program to determine females' responses to calls in the multidimensional space defined by several different acoustic properties. The multiple linear discriminant functions computed by a DFA thus provide an approximation of unknown accuracy for actual behavioral responses.

Regardless of whether female frogs' responses to parameters of advertising calls are unimodal or monotonic, a female's problem during mate choice remains similar in both cases. Both create the same kinds of possibilities for error (Wiley 1994). DFA is thus not so much a realistic model for a particular mechanism of species recognition as it is a general model for errors in recognition of signals.

DFA: the general issue of error in communication

Any mechanism for discrimination of signals, whether statistical, electronic, or biological, raises the problem of errors. Whenever different signals are not completely distinct, trade-offs are inevitable between false alarms and missed detections (Wiley 1994). Our results illustrate some consequences of these errors for the evolution of species recognition.

The most striking result of our DFAs concerns the use of multiple properties of calls for species recognition. No one acoustic property of calls in our analysis allowed discrimination of *H. ebraccata*'s calls without error. By including two properties of calls, the DFA reduced errors by half. Using all three properties, however, did not reduce errors further. Thus just two parameters of calls maximized discrimination of conspecifics. Even in this complex tropical anuran community, the DFA achieved nearly error-free discrimination with remarkably few parameters.

Fewer acoustic properties are required to classify calls of *H. ebraccata* than are necessary to classify songs of birds. Nelson and Marler (1990) studied the signal space of a community of birds in the eastern United States. A DFA required seven acoustic properties for flawless classification of field sparrow (*Spizella pusilla*) songs and three for chipping sparrow (*S. passerina*) songs. It is difficult to compare studies of frogs and birds, because it is uncertain that the properties of calls chosen for analysis have comparable significance for the subjects. Differences in the complex notes in birds' calls might prove to be more difficult to identify or to measure than the differences in frogs' calls. Nevertheless, there is a suggestion in these two studies that calls of syntopic frogs might overlap less than birds' songs.

A species on the periphery of signal space (like the chipping sparrow) might require fewer properties for accurate classification of its songs than would a species in the center of signal space (like the field sparrow) (Nelson and Marler 1990). Species of frogs also differ in the number of neighbors in acoustic space. *H. ebraccata*, for instance, has more neighbors in signal space than do other syntopic frog species (Figs. 3, 4). Comparisons with birds suggest that an acoustically peripheral species (such as *Scinax boulengeri*) might require only one acoustic property for near-perfect identification of conspecific calls.

Female frogs have a more focused objective than does a DFA. A female frog needs to identify only two classes of calls, conspecifics and heterospecifics. In contrast, our DFA divided calls into six classes, one for each species present. By specializing on the narrower task, females might evolve criteria for categorizing conspecific calls that would surpass the performance of a DFA. The results of our DFA, however, leave little room for improvement, as linear combinations of just two parameters allowed nearly flawless classification of the calls of *H. ebraccata*. One result of the DFA is thus the apparent redundancy in the differences among the calls of these species.

This redundancy might have important consequences in natural situations. Background sound makes detection and discrimination of calls less accurate (Wollerman 1999; Wollerman and Wiley 2002). In such noisy situations, it is possible that attention to additional parameters could be more important for reducing errors than our DFA indicated. For example, overlapping calls in choruses can obscure fine temporal features, such as pulse repetition rate (Schwartz 1987b, 1993). Under such conditions, attention to dominant frequency, which is less affected by call overlap, might be more important for reducing errors than a DFA of cleanly recorded calls would indicate. More study of females' responses in noisy and quiet conditions might clarify how combinations of acoustic features affect mate choice.

Females might also use cues other than males' calls to reduce errors during mate choice. For example, the DFA often confused calls of *H. ebraccata* with those of *H. loquax*. The latter, however, usually called from grasses in the center of the marsh, whereas *H. ebraccata* called from herbaceous vegetation at the periphery of the marsh (Donnelly and Guyer 1994). In Panama, male *H. ebraccata* prefer to call from higher, woodier, and more tangled vegetation and more permanent standing water than either *H. microcephala* or *H. phlebodes* (Fouqette 1960). Location would thus provide an additional cue by which females could distinguish conspecific males. Regardless of the location of males, females might have to pass calling heterospecific males in order to reach conspecific males. To assess the risks of errors in mate choice by frogs, we need to know more about the possibility of shifting tactics in search behavior of females.

Females could face conflicts in discrimination among species and among conspecifics, if the same acoustic properties of calls are used in both discriminations. Preferring calls with lower frequency can both increase a female's chances of mating with a larger conspecific male (Robertson 1986) and at the same time make her more susceptible to mismating with another species (Pfennig 2000). Female *H. ebraccata*, for instance, prefer lower dominant frequencies (at least within the range of conspecific calls) (Wollerman 1998), despite the possibility of greater confusion with *H. loquax*. However, the situation is complex in this tropical environment, because the preference for lower dominant frequencies (which loads heavily on factor 2 in Fig. 3a) would also reduce confusion with *Scinax elaeochroa*. Mechanisms for mate choice often must discriminate the optimal conspecific signal from multiple alternative sources of confounding stimulation.

Evolutionary divergence of calls in signal space

Nearest-neighbor analyses of species' means showed that advertisement calls were randomly located in discriminant function space. Yet we expected that species should evolve equidistant spacing of signals (with R approaching 2.15, Clark and Evans 1954). This prediction, however, seems less clear when we consider the probabilities of errors. The prediction assumes that false alarms and missed detections occur equally frequently and have equal payoffs for all species. As the separation of different species' signals increases, the possibilities for error would usually decrease, so selection for species distinctiveness would become progressively weaker. Nevertheless, if all errors are equally likely, the means should continue to evolve toward greater dispersion. In reality, however, the relative abundances of species affect both the probabilities and costs of both false alarms and missed detections.

The DFAs illustrate how the relative abundances of a species might influence the intensity of selection for species distinctiveness. The relative frequencies of species' calls, modeled by the prior probabilities of group membership, strongly influenced the type of errors committed by the DFA (Fig. 2b). Missed detections were the most common error when all species had the same prior probability. When these probabilities were unequal, more like those in the natural situation, error rates decreased overall, and most errors were false alarms. In essence, discriminant functions with unequal prior probabilities are more likely to include borderline cases with a common species (in our case, *H. ebraccata*) than with an uncommon species.

This result suggests that the relative abundance of a species could have complex consequences for female choice. The prior probability of hearing a conspecific signal is greater for common than for uncommon species. Thus for any threshold for response, females of a common species are more often correct when they perceive a conspecific signal than are females of uncommon species. This situation suggests that females of common species might evolve lower thresholds (in effect become less choosy in their responses to calls) (Wiley 1994). Although lower thresholds would increase the conditional probability of false alarms (responding to inappropriate males), females of common species might still have lower overall rates of error. On the other hand, costs of additional search are generally lower for females of common species, a situation that would favor a higher threshold and thus higher conditional probability of missed detections (passing by appropriate males). The relative abundance of a species could thus have counteracting effects on females' thresholds.

Rare species experience the opposite set of circumstances. For any given threshold, they are less likely to be correct when they perceive a conspecific call, and they probably experience higher costs of additional search. If calls at the periphery of signal space are easier to discriminate than those at the center (Nelson and Marler 1990), these considerations suggest that rare species might evolve calls farther from those of their nearest neighbors in acoustic space than would common species. Inspection of the locations of the species in discriminant function space (Figs. 3, 4) indicates that this expectation was fulfilled. *Smilisca baudinii* and *Scinax boulengeri*, the least common of the six hylid species, have calls that lie near the periphery of the signal space. *H. ebraccata*, by far the most numerous species, produces calls that lie near the center of the signal space. A larger sample of species is needed to confirm this possibility.

Relative abundances of species at La Selva change over the breeding season (Donnelly and Guyer 1994). All but one of the species included in both our and Donnelly and Guyer's (1994) studies are prolonged breeders. The exception, *Scinax elaeochroa*, is not encountered on most nights, but when it is present, it tends to be very common (Donnelly and Guyer 1994; personal observation). Appropriate thresholds of response for such explosively breeding species might be similar to that of common species because they are likely to be the most common species when breeding.

Selection for avoidance of other species in acoustic space is more complicated than anticipated. A comparison of species recognition by common and rare species might reveal the consequences of prior probabilities and of trade-offs between false alarms and missed detections.

Conclusion

Application of DFA to this community of tropical hylid frogs illustrates the problems of signal discrimination in complex acoustic environments. No single parameter of calls served to eliminate the possibility of errors for a common species, although, at least for calls with little background energy, combinations of no more than two parameters often did eliminate error. The consequences of unequal abundance of coexisting species for signal discrimination suggest that common and rare species might evolve different adaptations to reduce errors.

By directing attention to the problems of errors in communication, this analysis has indicated some ways to advance our understanding of species recognition and other forms of communication. In particular we need to know more about how errors in communication are affected by (1) redundancy in signal parameters, (2) background stimulation from extraneous sources, (3) shifts in recipients' tactics while searching for signals, (4) multiple sources of confounding stimulation, and (5) prior probabilities of signals as determined by a species' relative abundance.

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