

SPECIES RECOGNITION AND SEXUAL SELECTION AS A UNITARY PROBLEM IN ANIMAL COMMUNICATION

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Abstract.—We investigated patterns of mating call preference and mating call recognition by examining phonotaxis of female túngara frogs, *Physalaemus pustulosus*, in response to conspecific and heterospecific calls. There are four results: females always prefer conspecific calls; most heterospecific calls do not elicit phonotaxis; some heterospecific calls do elicit phonotaxis and thus are effective mate recognition signals; and females prefer conspecific calls to which a component of a heterospecific call has been added to a normal conspecific call. We use these data to illustrate how concepts of species recognition and sexual selection can be understood in a unitary framework by comparing the distribution of signal traits to female preference functions.

Key words.—Female choice, mate recognition, mating preferences, *Physalaemus pustulosus*, sexual selection, species recognition.

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Species recognition and sexual selection are both essentially problems in animal communication and can result from how females respond to variation in male traits. These theories often are viewed as antithetical, however, and Cronin (1992) has suggested this apposition has hindered our understanding of both processes. For example, some researchers have contended that sexual selection is unlikely to be an important force in signal evolution because species recognition would generate strong stabilizing selection on mate recognition systems, suggesting that if there is species recognition there can not be sexual selection (Templeton, 1979; Gerhardt, 1982; Paterson, 1985). This clearly need not be the case because there are hundreds of studies that now demonstrate strong directional selection on various components of signals used to attract conspecific mates (Ryan and Keddy-Hector, 1992) and considerable variation in signals and receivers among populations of the same species (Claridge et al., 1988; Verrill and Arnold, 1989; Ritchie, 1991; Ryan and Wilczynski, 1991; Ryan et al., 1992).

It seems that this unfortunate misunderstanding has arisen from several causes. One is imprecise definition. A second is implying cause from effect. And a third reason is that

many studies concentrate on the problems of either species recognition or sexual selection, a myopia that hinders an appreciation for how these phenomena interact.

We have been studying the evolution of communication in frogs of the *Physalaemus pustulosus* species group. Initial studies concentrated on how variation within a population influences female mating preferences (Ryan, 1980; Rand and Ryan, 1981; Ryan, 1985; Ryan and Rand, 1990; Rand et al., 1992). These studies have now been extended to determine how variation both within and among species influences preferences (Ryan et al., 1990; Ryan and Rand, 1993). As such, these studies span topics in both sexual selection and species recognition. Results from these studies emphasize the commonalities rather than the disparities between these phenomena. We use these results to illustrate how concepts of recognition, preference, and sexual selection can be understood in a unitary framework by comparing the distribution of signal traits with the female preference function.

Operational Definitions

Much of the problem in unifying species recognition and sexual selection may be one of definition. We are concerned with behavioral responses to advertisement signals

in the context of mating. Thus we define mate recognition as a behavioral response indicating that one individual considers another an appropriate mate, even if mistakenly. This definition can be applied to species recognition as well as to recognition of sex, relatives, or populations. It does not imply preference or comparison, and in that sense adheres to the definition of mate recognition proposed by Paterson (1985).

Mate preference, on the other hand, is a behavioral response indicating that an individual intends to mate with one individual rather than another. This definition can be utilized in discussions of species preferences and in the preferences females show among conspecific males in sexual selection. Preference is distinguished from recognition in that it implies a comparison. For example, in the túngara frog, *P. pustulosus*, males produce a whine or a whine followed by chucks. Either call alone will elicit positive phonotaxis from a female; thus both are recognized as signaling an appropriate mate. When given a choice between the two stimuli, females prefer the call with chucks; both are recognized, one is preferred [this distinction is also emphasized by Ewing (1988, p. 167)]. We believe this definition of preference is very much in the spirit of discussions of behavioral mechanisms in both speciation (e.g., Dobzhansky, 1937; Mayr, 1988; Otte and Endler, 1989) and in sexual selection (Fisher, 1958; Bradbury and Andersson, 1987; Kirkpatrick and Ryan, 1991).

We define sexual selection as variance in reproductive success that derives from variation in the ability to acquire mates; here, we are concerned with variation in male mating success that arises from female mating preferences. This definition reflects the original discussion by Darwin (1871) and is not considered controversial (e.g., Bradbury and Andersson, 1987; Cronin, 1992).

It is important to note that these definitions do not assume any particular causal agent. If females recognize their own males as appropriate mates and if they prefer these males to heterospecifics, this information alone would not allow us to discriminate between theories of reinforcement (Dobzhansky, 1937; Littlejohn, 1981) and incidental divergence in allopatry (Mayr, 1988;

Paterson, 1985) as the cause for these behavioral responses by females. Analogously, if females prefer some conspecific males over others, then sexual selection occurs when this preference generates variance in male mating success, but the mere existence of sexual selection does not allow us to discriminate the several hypotheses positing why females would evolve such preferences (e.g., good genes, runaway sexual selection, or sensory exploitation; Kirkpatrick and Ryan, 1991), an issue Darwin (1871) considered in detail.

Mate recognition and mate preference can result from an interaction between variation in signals and responses to signal variation, which can be represented as preference functions. This interaction can cause non-random mating associations both among and within species. This is true regardless of the evolutionary forces that have influenced signal structure and preference functions. Unfortunately, most studies, including most of our own, do not consider the effect of signal variation both within and among species, and they usually are restricted to considering only recognition or preference but not both. In many studies of species recognition, simultaneous choice tests illustrate that females prefer conspecific signals but these studies do not consider if the conspecific signal would be recognized as identifying an appropriate mate, even though in some studies of insects (Ewing, 1988) and frogs (Gerhardt, 1988) heterospecific signals are recognized as appropriate. We have conducted studies of the *Physalaemus pustulosus* species group in which we have tested for both recognition and preference, and we use these data to explore the relationship between species recognition and sexual selection.

The Physalaemus pustulosus Species Group

The genus *Physalaemus* (Family Leptodactylidae) as currently defined contains about 30 species (Frost, 1985). Cannatella and Duellman (1984) defined the *Physalaemus pustulosus* species group as consisting of four species: *P. pustulosus*–*P. petersi* are east of the Andes (*P. pustulosus* is also found in Central America), and *P. coloradorum*–

P. pustulatus are restricted to the western side of the Andes in Ecuador and Peru. *P. pustulatus* was considered to encompass populations in both Ecuador and Peru (Cannatella and Duellman, 1984), but recently we showed that the populations in these two countries differ substantially in morphology, allozymes, and mitochondrial DNA sequence, as well as calls (Cannatella et al., unpubl. data). The populations in Peru will be named a new species, which we refer to here as *P. "pustulatus-Peru."*

We determined the phonotactic responses of female *P. pustulosus* to the calls of these species as well as three other species that are close relatives of the species group: *P. enesefae*, *P. ephippifer*, and an as yet undetermined taxa we refer to as *P. "roraima."* All of these species are allopatric with *P. pustulosus* except for an area of sympatry with *P. enesefae* in the llanos of Venezuela. More detailed information on the geographic ranges of these species is given in Ryan and Rand (1993).

All species tested have advertisement calls that consist of a relatively low-frequency fundamental (< 1,000 Hz) that sweeps downward to at least half its starting frequency over a duration of 80 to 400 msec (Fig. 1). *P. pustulosus* is able to add chucks to the whine. These chucks enhance the attraction of the call to females but are neither necessary nor sufficient for species recognition (Ryan, 1985). In some populations *P. petersi* also adds a chuck-like suffix, but chucks are absent in all other species in the group and have not been reported in any of the other species in the genus. Our current understanding of the phylogeny of the species group [Cannatella and Duellman, 1984; data on allozymes and mtDNA sequence (Hillis et al., unpubl. data)] suggests that the chuck was derived independently in *P. pustulosus* and some populations of *P. petersi* and was never present in ancestors of other species in the group.

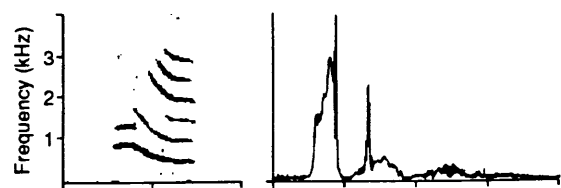
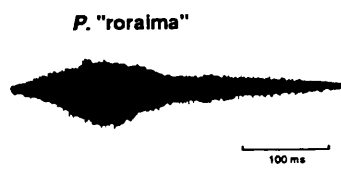
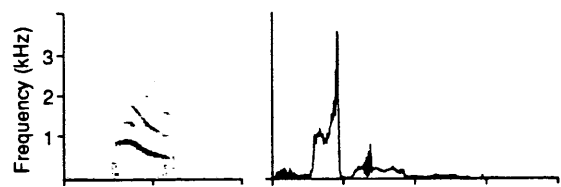
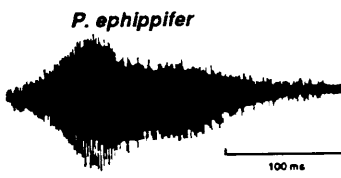
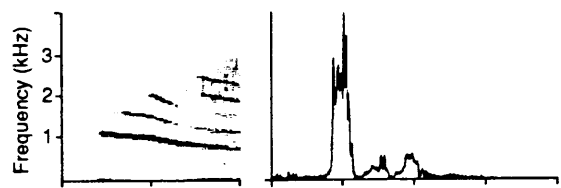
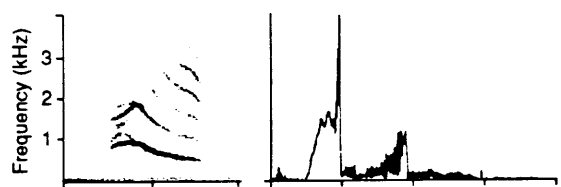
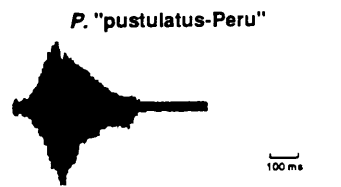
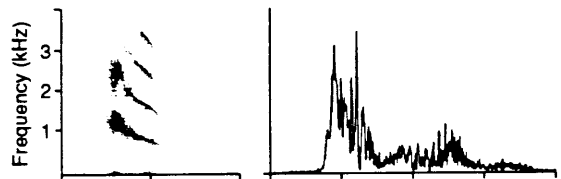
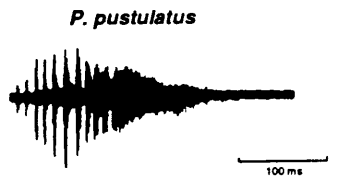
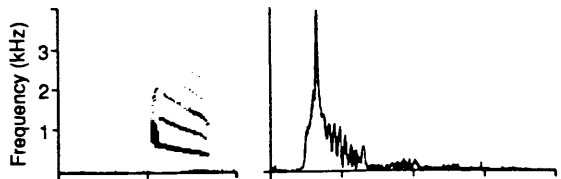
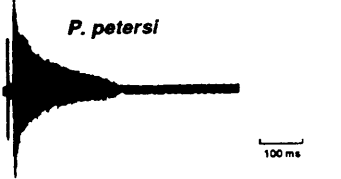
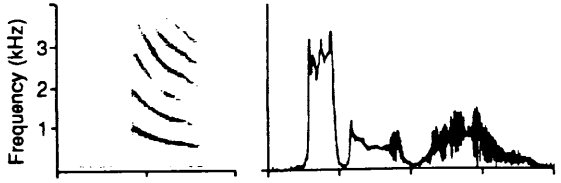
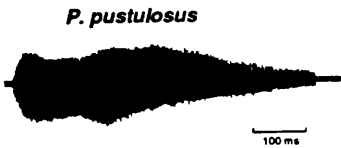
Ryan and Rand (1993) showed that when female *P. coloradurum* were given a choice between the whine-like conspecific call and the same call to which chucks from *P. pustulosus* were appended they preferred the latter. This suggests that the preference for chucks characterized a common ancestor of *P. coloradurum* and *P. pustulosus* and thus

existed prior to the evolution of the chuck. This supports the hypothesis of sensory exploitation, which states that males can evolve traits that exploit preexisting female preferences (Ryan, 1990). *P. pustulatus* also has a component unique to its call. This is an amplitude modulated sound of similar duration as the *P. pustulatus* whine (Fig. 1). It differs from the chuck in many acoustic parameters, and also in that it occurs before rather than after the whine and that its presence is fixed rather than variable. Similar to the sensory exploitation experiments described above with *P. coloradurum* preference for *P. pustulosus* chucks, we also determined preference of *P. pustulosus* females for a conspecific call to which the prefix from the *P. pustulatus* call was appended.

MATERIALS AND METHODS

Female *P. pustulosus* were studied in Gamboa, Panama. Calls of all species tested were recorded by us in the field or obtained from the U.S. National Museum of Natural History (*P. "roraima"*). We used natural calls except for the *P. pustulosus* call in which case we used a synthetic signal. We also created a call in which the prefix of a natural *P. pustulatus* call was appended to the *P. pustulosus* whine. The noise stimulus was randomly generated white noise with the duration and amplitude envelope of the "whine" portion of the advertisement call of *P. pustulosus*.

Female phonotaxis experiments were conducted during 1990 and 1991 as in Ryan and Rand (1990). Calls were digitized on an Amiga computer (model 2000). Calls of each stimulus pair were broadcast through one of the channels of the computer to an ADS L200C speaker. Calls were presented antiphonally, each call at a rate of 1 call/2 sec. Speakers were placed directly opposite one another, 3 m apart, in a small room in which the walls were covered with foam to reduce acoustic reverberation. Stimuli were broadcast at peak intensity of 82 dB SPL at the site of the female. A female was placed equidistant between the speakers under a funnel. After two minutes the female was released and a response was noted if she approached to within 10 cm of a speaker. A "no response" was scored if the female remained



.4 .8 1.2 0 1000 2000 3000 4000
Time (sec) Frequency (Hz)

motionless for 5 min or if she did not exhibit phonotaxis within 15 min.

Statistical analysis was by exact binomial probability. We used a one-tailed test when analyzing the choices between conspecific and heterospecific calls because we predicted preference for conspecific calls. We also used a one-tailed test when comparing the *P. pustulosus* call to which the *P. pustulatus* prefix was added; in this case sensory exploitation predicts a preference for the altered call. We used a two-tailed test when comparing responses to heterospecific calls, noise, and "no responses" (see below) because no a priori predictions were made.

Female preference was determined as in most studies (e.g., Ryan and Rand, 1990); females were presented a pair of stimuli. To determine recognition, however, a female must be presented with only one relevant stimulus; this stimulus was paired with white noise to determine if females were merely responding to any sound. Significant phonotaxis for the heterospecific call demonstrates this is a stimulus sufficient for eliciting female phonotaxis. Random responses to the heterospecific call and the noise suggest that females are merely responding to sound, and that the heterospecific call is not a sufficient stimulus for mate attraction. However, the lack of phonotaxis could result either from females being unresponsive to any stimulation, for example due to lack of motivation, or because neither of the stimuli was biologically meaningful. In these heterospecific call versus noise experiments, all females tested had first responded to a conspecific call in a previous test. If a female later did not respond to either the heterospecific call or the noise, this was scored as a "no response" only if the female then showed a phonotactic response in a subsequent test. Such cases, we feel, demonstrate that lack of response is more likely due to lack of appropriate acoustic stimulation rather than to lack of motivation.

The null hypothesis was determined by Rand et al. (1992). They presented 20 females with two speakers located in their normal positions in the playback arena. One

speaker broadcast noise and the other was silent. The number of times a female approaches a silent speaker estimates the number of times that a female would happen to approach by random chance without reference to the stimulus being broadcast. Eighteen females showed no response (as defined above) and two came into contact with the silent speaker. Thus if females ignore the heterospecific call as a communication signal the null expectation is that they would still approach the call by chance in the ratio of 2:18. This expectation was compared to the actual responses with a Fisher's exact test.

RESULTS

Female *P. pustulosus* showed statistically significant, almost unanimous preferences for the conspecific call over the calls of the other seven heterospecifics (Fig. 2). In seven separate experiments involving 74 phonotactic responses, only once did a female respond to a heterospecific call. Clearly, females prefer conspecific calls to those of all heterospecifics tested.

The calls of three species, *P. pustulatus*, *P. petersi*, and *P. enesefae* never elicited phonotaxis from female *P. pustulosus* in a total of 34 tests in which females were presented with a heterospecific call and noise (Fig. 3). In all of those tests, a female responded to noise only once.

In two experiments female *P. pustulosus* showed statistically significant phonotactic responses to the heterospecific call (Fig. 3). In response to calls of *P. coloradurum* and *P. "roraima,"* females showed identical responses: they responded to the heterospecific call eight times, never to noise, and only twice did females approach neither stimulus. Thus the calls of both *P. coloradurum* and *P. "roraima"* are effective stimuli for eliciting phonotaxis from female *P. pustulosus*. The calls of *P. ephippifer* and *P. "pustulatus-Peru"* elicited some phonotactic responses, but no more than was expected by chance (Fig. 3).

Female *P. pustulosus* did not show a preference for the normal conspecific call over

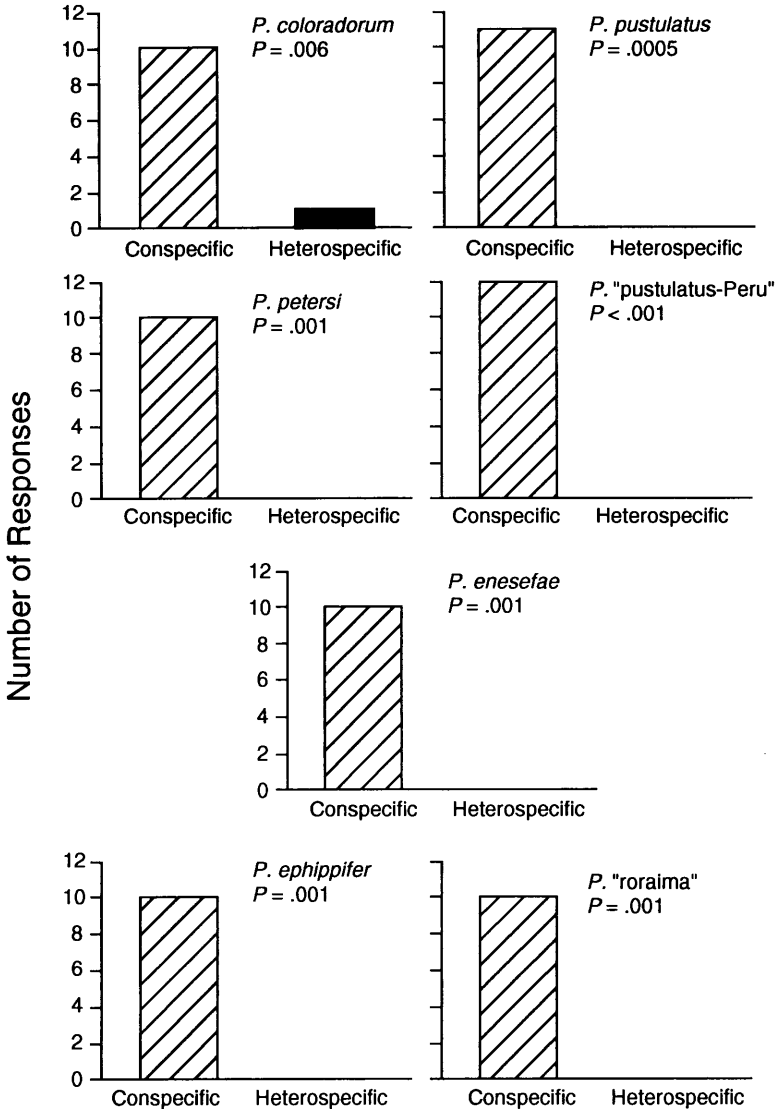
Physalaemus pustulosus

FIG. 2. Phonotactic responses of female *Physalaemus pustulosus* to conspecific and heterospecific calls.

the same call to which a heterospecific component, the *P. pustulatus* prefix, had been added. In this case the heterospecific prefix was preferred to the conspecific condition, which is that of no prefix (Fig. 4).

DISCUSSION

This study yields four results. First, there is unanimous preference for conspecific calls relative to heterospecific calls. Second, most heterospecific calls are ineffective signals for

eliciting phonotaxis. Third, some heterospecific calls are effective signals; they are recognized as signaling an appropriate mate. Fourth, females show a preference for a heterospecific call component when added to the call of conspecifics. We consider how various interactions of the signal with the preference function of the receiver could explain these results.

Figure 5 illustrates in univariate space the signals of two species and several possible

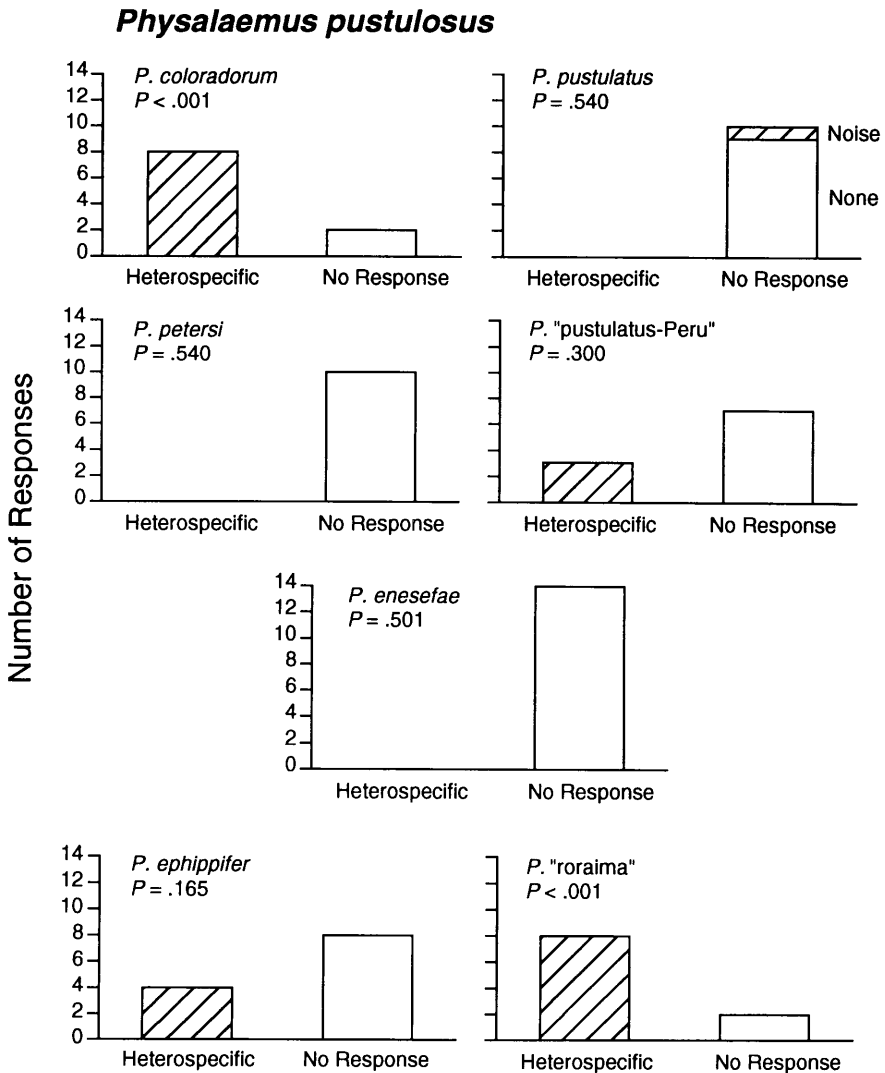


FIG. 3. Phonotactic responses of female *Physalaemus pustulosus* to heterospecific calls and noise.

receiver functions for one of the species. We use this figure as a heuristic to interpret our results, as well those of other studies, that show contrasting patterns of female responses to signal variation at different levels. We emphasize that in reality signals and receivers vary along many axes and only an exhaustive study of all axes of variation can provide precise information as to how signals and receivers interact. Nevertheless, we also believe that some patterns are apparent enough to be amply demonstrated by this simple model.

The preference functions a through d il-

lustrated in Figure 5 would all result in female preference for the conspecific signal relative to the heterospecific signal illustrated, but would differ in how they would influence preferences among conspecific and responses to only heterospecific signals. Functions a through c would all result in no response to heterospecific signals; function a would not generate selection on conspecific signals, while functions b and c would generate stabilizing and directional selection, respectively, as well as species-specific preferences. We know of no cases of a signal-receiver interaction as in function a; that

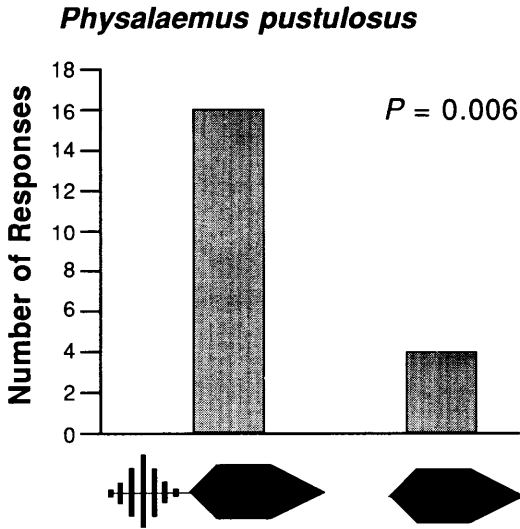


FIG. 4. Phonotactic responses of female *Physalaemus pustulosus* to a normal conspecific call and that call to which the prefix of the *P. pustulosus* calls was appended.

is a preference function that is not influenced by conspecific signal variation and completely ignores heterospecific signals. Such an absence of data might be because many studies concentrate on comparisons between species or variation within populations, but usually not both. For example, in our study the majority of experiments reveal both a preference for conspecific signals and no response to heterospecifics. This result would coincide with functions a through c (Fig. 5), but would not allow us to discriminate among them. There are several examples of the relationship illustrated by functions b and c. For example, Gerhardt (1991) shows that in gray treefrogs, *Hyla versicolor*, preferences tend to generate stabilizing selection (function b; Fig. 5) on some call properties (e.g., pulse rate) and directional selection (function c) on others (e.g., dominant frequency). Ryan and Keddy-Hector (1992) also review numerous cases of directional female preferences for male secondary sexual characters (function c; Fig. 5).

Function d (Fig. 5) illustrates that females would prefer conspecific to heterospecific signals, but that a heterospecific signal would still elicit a response. In this study, the responses of *P. pustulosus* to heterospecifics are examples of such a phenomenon, and

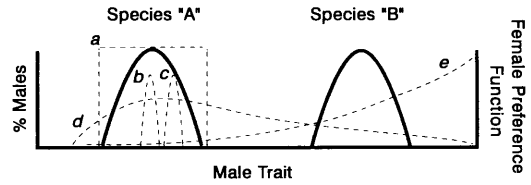


FIG. 5. Hypothetical interactions between variation in a male trait and female preference functions. The solid lines show the distribution of variation in male traits for species "A" and species "B." Female preference functions (a-e), which show the strength of the preference as a function of variation in the trait, are shown in the dashed lines for females of species "A."

Ryan and Rand (1993) show that female *P. coloradorum* also exhibits phonotaxis to some heterospecific calls. Similar results have been found in other species as well. For example, bush crickets respond to signals of heterospecifics that are allopatric although not those that are sympatric (Gwynne and Morris, 1986). And Brenowitz (1991) showed that female canaries prefer conspecific song to heterospecific song, but both songs elicit similar responses when a song nucleus (HvC) is lesioned, suggesting that recognition and preference might take place at different levels of neural organization.

Finally, function e (Fig. 5) illustrates that females could respond to the conspecific signal but could prefer the heterospecific signal and other signals outside of the species' range if it is a super-normal stimulus. There are several examples of preferences for super-normal signals, although these signals do not resemble those of heterospecifics. For example, male fritillary butterflies choose females on the basis of wing beat frequency, and they prefer frequencies of 140 Hz, although the maximum wing beat of females was only 10 Hz (Magnus, 1958). In another example, Gerhardt (1991) showed open-ended preferences for call duration in *H. versicolor*. Ryan and Keddy-Hector (1992) review several other examples of preference for supernormal stimuli, a well-known idea in ethology (Tinbergen, 1953).

Preferences for signals outside of the species range could result in the unusual phenomenon of preference for heterospecific signals over conspecific signals; such preferences occur in the *Physalaemus* lineage.

As we discussed above, only *P. pustulosus* and some populations of *P. petersi* add chucks to their call, but *P. coloradorum* females prefer a conspecific call to which chucks were added over the normal chuckless call of their own males (Ryan and Rand, 1993). Also, male *P. coloradorum* sometimes produce calls in doublets and triplets, a trait that is not exhibited by *P. pustulosus* males. When given a choice between single and multiple calls, however, female *P. pustulosus* prefer the latter (Ryan and Rand, 1993). In this study we showed that *P. pustulatus* has a call component, one that precedes the whine, that is not present in the other species studied. Female *P. pustulosus* prefer their own call to which this prefix has been added over their own normal conspecific call. Thus in the *Physalaemus pustulosus* species group there are several examples of females preferring call components or call patterns exhibited by heterospecifics and not exhibited by their own males. These cases do not suggest preference for heterospecific calls in nature (if they were to occur in sympatry) because these heterospecific components are not attractive until appended to the conspecific call. These results do suggest, however, that there are preferences that would favor the evolution of these heterospecific traits if they were to evolve in conspecifics, and offers support for the sensory exploitation hypothesis (Ryan, 1990).

Preferences for heterospecific traits have been documented in other species as well. Basolo (1990) showed that female platyfish (genus *Xiphophorus*) prefer males to which swords were appended to the tail. This trait is absent among platys but characterizes the congeneric swordtails. Also with *Xiphophorus*, Ryan and Wagner (1987) showed that female swordtails, *X. pygmaeus*, prefer heterospecific males, *X. nigrensis*, to their own males; the heterospecifics are both larger and exhibit courtship displays that are absent in *X. pygmaeus*. In other examples, a bush cricket (*Conocephalus nigropleurum*) prefers a faster, heterospecific calling rate to its own (Morris et al. 1978); and in birds, Searcy (1992) demonstrated that female grackles prefer song repertoires even though their own males produce only single call types.

Particular interactions of a preference function within conspecific and heterospecific signal properties will yield different patterns of mating, including species-specific preferences, conspecific preferences, recognition of heterospecific signals as appropriate, and sometimes heterospecific preferences. We emphasize that species recognition and sexual selection are the result of the interactions of signals and receivers and these patterns of nonrandom mating need not reveal why they evolved.

We have not addressed why signals and receivers have particular properties. There is considerable debate as to what evolutionary forces bring about species recognition (Otte and Endler, 1989) and the preferences involved in sexual selection (Kirkpatrick and Ryan, 1991), but it seems clear that selection in one circumstance can have unintended consequences in another circumstance. For example, there might be selection to mate with conspecifics to avoid hybridization with heterospecifics (e.g., Dobzhansky, 1937), but if there is variance in the species-specific signals of males or variance in the species-specific preference function of females this could generate sexual selection (Fisher, 1958; consider Fig. 5, functions b through d). Although it has been difficult to elucidate the reasons why females exhibit certain preferences, the inability to understand why females choose does not detract from the fact that such choice exists; sexual selection can be generated whether or not we understand why.

We suggest that nonrandom patterns of mating can result from particular interactions between signals and receivers, and especially that species recognition and sexual selection are not antithetical. It is helpful to acknowledge this fact clearly, before attempting the more difficult and perhaps more interesting task of determining the specific forces that have caused signals and receivers to have certain parameters.

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