CHAPTER

15

Phylogenetic patterns of behavioural mate recognition systems in the *Physalaemus pustulosus* species group (Anura: Leptodactylidae): the role of ancestral and derived characters and sensory exploitation

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Abstract
We have investigated patterns of mate recognition in a group of closely related frogs in which, in most cases, divergence appears to have occurred in allopatry with no secondary contact. We infer the influence of derived and ancestral characters in communication between the sexes by determining female phonotactic responses to conspecific versus heterospecific calls, only heterospecific calls, and call characters

that influence intraspecific mate choice. We test the phonotactic responses of females of two species to the calls of six species: four are in the same species group and two are closely related to the species group.

In all cases females preferred conspecific to heterospecific calls, suggesting that characters of the communication systems derived in allopatry are sufficient to ensure species mate recognition. Females are attracted to some heterospecific calls; thus shared, perhaps ancestral, characters of the systems can allow effective communication between heterospecifics. Finally, call characters that enhance mate attraction in two lineages also enhance call attraction in a lineage that lacks this call character. This intraspecific preference appears to be an ancestral character of the receiver that existed before the evolution of the call character that enhances attraction. This result is consistent with the hypothesis that males can evolve traits to exploit already existing preferences (sensory exploitation).

INTRODUCTION

Many animals exhibit assortative mating among species. This can result from conspecific males and females sharing a communication system in which males produce species-specific signals and females exhibit a preferential response to the signals of conspecifics relative to those of heterospecifics. Thus conspecific mate recognition is an interaction of both the specificity of the male signal and the female preference. Much debate on the evolution of mate recognition systems has concerned how this species specificity evolves during secondary contact (Littlejohn, 1981; Paterson, 1982; Mayr, 1988).

We emphasize several issues in our studies of the evolution of mate recognition systems that are often neglected in other studies. First, we consider the degree to which these systems diverge in allopatry rather than sympatry or parapatry, because we feel this is a common mode of speciation (Mayr, 1988). Second, we point out that although the divergence of mate recognition signals is of obvious importance, it is the interaction of the signal and the receiver that results in mate recognition. Third, although signals and receivers might exhibit species-specific and thus derived characters, each is a multivariate trait composed of a constellation of ancestral and derived characters, the importance of which might vary with the communication context. Fourth, although there is often close concordance between properties of the signal and receiver, the evolution of signals and receivers need not be genetically linked (Butlin, 1989), and in some cases the sequence of signal–receiver evolution could suggest that males evolve signals to exploit already existing biases in the receiver (Ryan, 1990a).

In this study we use female phonotaxis experiments to address these issues in a group of closely related frogs. Specifically, we determine: (1) if differences in the communication system are sufficient for species discrimination; (2) if similarities in these systems allow effective heterospecific communication; and, (3) if traits that characterize one lineage are effective for communication in another lineage.

Anuran mate recognition

Certain aspects of how conspecific mate recognition operates are well-understood in frogs (Fuzessery, 1988; Gerhardt, 1988; Rand, 1988; Walkowiak, 1988; Ryan, 1991). Males produce advertisement calls, one function of which is to attract females.

Although there can be substantial and biologically meaningful call variation within a species, it is usually small relative to the variation among species (Ryan, 1990b). In that sense (i.e. in partitioning intra- versus interspecific call variation, as opposed to attributing to the call an evolved function), the advertisement call is 'species specific'. Many studies of frogs have shown that when given a choice between calls of conspecifics and heterospecifics, females exhibit preferential phonotaxis to the conspecific call (Gerhardt, 1988). Furthermore, studies of anuran auditory physiology have revealed that neural properties of this system can exhibit a preferential bias towards the spectral and temporal properties of the conspecific advertisement call (Fuzessery, 1988; Walkowiak, 1988; Zakon & Wilczynski, 1988).

Females also exhibit mating preferences among conspecific males (Gerhardt, 1988; Ryan, 1991; Ryan & Keddy-Hector, 1992), and in some cases the neural properties of the auditory system can also explain intraspecific mating preferences. For example, in *Hyla versicolor* (Gerhardt & Doherty, 1988), *Physalaemus pustulosus* (Ryan *et al.*, 1990) and *Acris crepitans* (Ryan, Perrill & Wilczynski, 1992) females prefer calls with frequencies that are lower than the population average, and the female's peripheral auditory system is tuned to these lower frequencies.

The *Physalaemus pustulosus* species group

The genus *Physalaemus* (Family Leptodactylidae) as currently defined contains about 30 species (Frost, 1985). The *Physalaemus pustulosus* species group, as defined by Cannatella & Duellman (1984), consists of four species in two species pairs.

One species pair consists of *P. pustulosus* and *P. petersi. P. pustulosus* is distributed throughout much of Central America as well as Colombia, Venezuela and Trinidad (Fig. 1). *P. petersi* is distributed widely throughout Amazonia and is found in Colombia, Ecuador, Peru, Bolivia and Brazil. The ranges of the two species are allopatric; their closest proximity is in Colombia, where they occur within several hundred kilometres of one another (Fig. 1). Both species are sympatric with other members of the genus. *P. pustulosus* is sympatric with *P. enesefae* in the ilanos of Venezuela, and *P. petersi* is sympatric with *P. ephippifer* near the mouth of the Amazon River in the region of Belen, Brazil. Further exploration might show *P. petersi* to be sympatric or parapatric with other congenerics, this seems less likely for *P. pustulosus.*

The other two species of the group have more restricted distributions (Fig. 1). *P. coloradorum* is found in low to mid-elevation rain forests on the western slope of the Andes in Ecuador. *P. pustulatus* ranges from southern Ecuador to northern Peru in the drier regions along the Pacific coast. Preliminary evidence suggests that *P. pustulatus*, as currently described, might consist of two species; we foresee the population from Peru being described as taxonomically distinct (Cannatella *et al., unpublished data*). Here, all experiments with calls of *P. pustulatus* refer to the Ecuadorian populations.

The ranges of *P. coloradorum* and *P. pustulatus (sensu lato)* are also allopatric, approaching within 200 km in western Ecuador. Being the only representatives of the genus west of the Andes, these species are isolated from any other congenerics, and probably have been since the late Tertiary (Cannatella & Duellman, 1984).

We use two species that are closely related to the *P. pustulosus* species group for outgroup comparisons. *P. enesefae*, as mentioned above, is sympatric with *P. pustulosus* in Venezuela. *P. 'roraima'* is an undescribed species from the northern-most state of
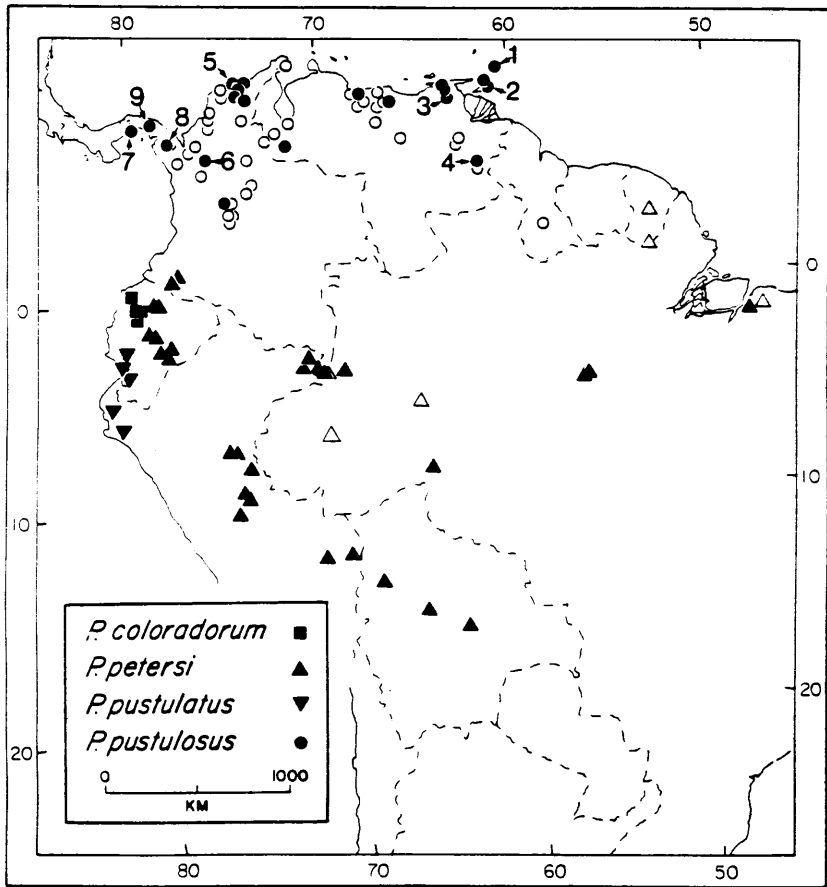
Figure 1 The distribution of members of the *Physalaemus pustulosus* species group. Localities of *P. pustulosus* in northern Central America are not included. (From Cannatella & Duellman, 1984.)

Roraima in Brazil. Its range is situated to the north of *P. petersi* and to the south of *P. pustulosus*. Although its taxonomic and phylogenetic status are not yet resolved, to us it appears most similar to *P. ephippifer*, and as such is probably closely related to but not a member of the *P. pustulosus* species group.

All species tested have advertisement calls that consist of a relatively low-frequency fundamental (< 1000 Hz) that sweeps downward to at least half its starting frequency over a duration of 80–300 ms (Ryan & Drewes, 1990; Fig. 2). All species differ in at least the initial and final frequency and duration of the call. *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 chucks. Nothing is known of the function of the chuck in this species.

MATERIALS AND METHODS

Female *P. coloradorum* were studied in Tinalandia, near Santo Domingo de los Colorados, Ecuador. Female *P. pustulosus* were studied in Gamboa, Panama; results
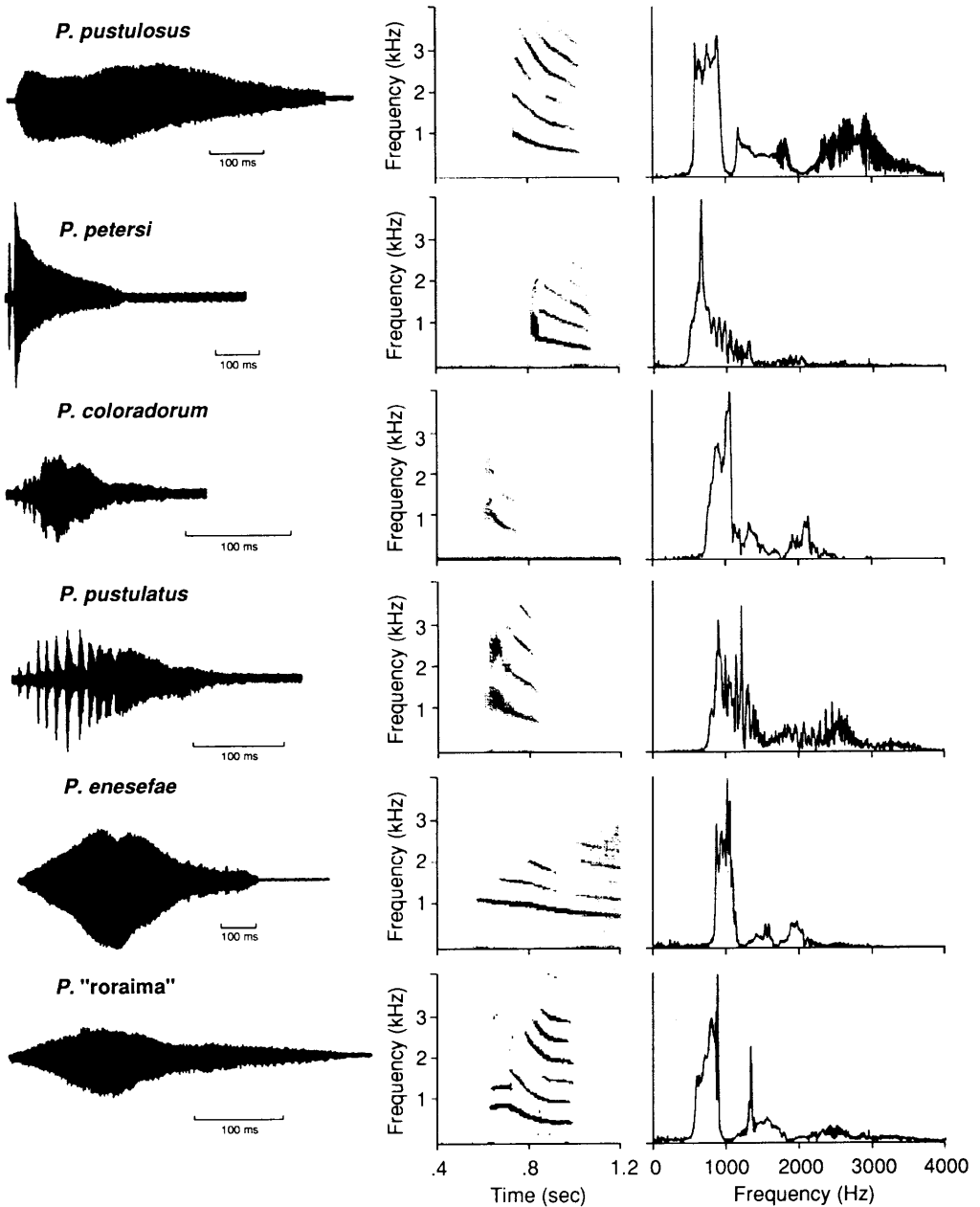
Figure 2 Oscillograms, sonograms, and fourier transforms of the advertisement calls of the species used in this study. (Figure 2a from Ryan & Drewes, 1990.)

of these studies have been published elsewhere (Ryan & Rand, in press), but are included here to facilitate comparisons. All calls used were recorded by us in the field or obtained from the U.S. National Museum of Natural History (*P.* 'roraima' and *P. enesefae*). 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 similarly in Ecuador and Panama (see also Ryan & Rand, 1990, in press; Rand, Ryan & Wilczynski, 1992). Experiments were conducted in 1990 and 1991. Calls were digitized on an Amiga computer (models 500 or 2000). Calls of each stimulus pair were played 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 per 2 s. Speakers were placed directly opposite one another (3 m apart in Panama, 1.4 m in Ecuador) in a small room the walls of which were covered with foam to reduce acoustic reverberation. Stimuli were broadcast at a peak intensity of 82 dB sound pressure level re 20 microPascals at the site of the female. A female was placed equidistant between the speakers under a funnel. After 2 min the female was released and a response was noted if she approached to within 10 cm of a speaker.

Statistical analysis was by exact binomial probability test. We used a one-tailed test when analysing the choices between conspecific and heterospecific calls, and between normal calls and calls to which characters that enhance attraction in other species had been added since there is an a priori prediction of the direction of the response.

Here, we do not treat the responses of females to heterospecific calls and noise statistically. This is because the null hypothesis is not 0.5 versus 0.5, and must be determined experimentally. Rand, Ryan & Wilczynski (1992) have done this for *P. pustulosus*, but it has not been done for *P. coloradorum*. Nevertheless, the patterns of response are quite clear without statistical treatment.

Interpreting female behaviour was more difficult when she was presented with a choice between a heterospecific call and noise. A significant preference for the heterospecific call shows that this is a stimulus sufficient for eliciting female phonotaxis. Random response to the heterospecific call and the noise would 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 either stimulus, for example due to lack of motivation, or because neither of the stimuli was biologically meaningful. If a female did not respond to either stimulus, this was counted 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 not due to lack of motivation, but rather to lack of appropriate acoustic stimulation (see also Rand, Ryan & Wilczynski, 1992; Ryan & Rand, in press.

RESULTS

Interspecific call preferences

As noted above, phonotaxis experiments with *P. pustulosus* have been published elsewhere (Ryan & Rand, in press) but are included here to facilitate comparisons. Females of both *P. pustulosus* and *P. coloradorum* showed statistically significant, almost unanimous preferences for the conspecific call over the calls of the other five heterospecifics (Figs 3 and 4). In ten separate experiments involving 88 phonotactic responses, only three times did a female respond to a heterospecific call.

In most cases, female *P. pustulosus* ignored both the heterospecific calls and the
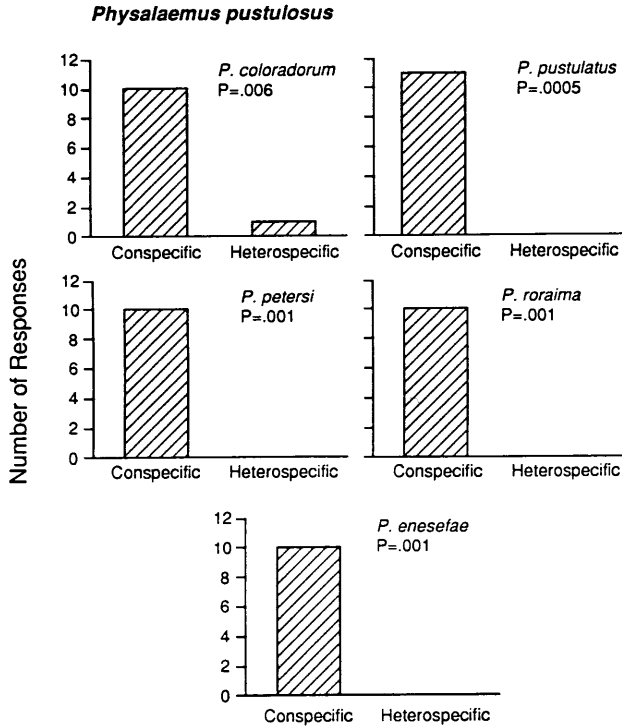
Figure 3 Phonotactic responses of female *Physalaemus pustulosus* to conspecific versus heterospecific calls.

noise stimulus. The calls of *P. pustulatus, P. petersi* and *P. enesefae* never elicited phonotaxis from female *P. pustulosus* in a total of 34 tests (Fig. 5). In all of those tests, a female responded to the speaker broadcasting noise only once. In the other 33 cases the females responded to stimuli in subsequent tests; thus their lack of response when confronted with heterospecific calls and noise was deemed to be due to the inappropriateness of the stimuli rather than lack of motivation due to physiological state.

In two cases female *P. pustulosus* showed statistically significant phonotactic responses to the heterospecific call (Fig. 5). In response to calls of *P. coloradorum* and *P.* 'roraima', females responded to the heterospecific call eight times, never to the noise, and only twice did females who approached neither stimulus subsequently exhibit phonotaxis in another test. Thus the calls of both *P. coloradorum* and *P.* 'roraima' are effective stimuli for eliciting phonotaxis from female *P. pustulosus.*

Female *P. coloradorum* differed from *P. pustulosus* in that they were more likely to approach a speaker broadcasting noise. Usually, in each experiment females approached the noise stimulus once or twice; in one experiment they approached the noise four times. They also showed more responses to the heterospecific calls (Fig. 6). However, unlike *P. pustulosus*, female *P. coloradorum* never showed more responses to the heterospecific call than 'no responses', as defined above.

It is intriguing that female *P. coloradorum* showed more responses to the *P. pustulosus* call than to any other heterospecific call. This bias is not statistically
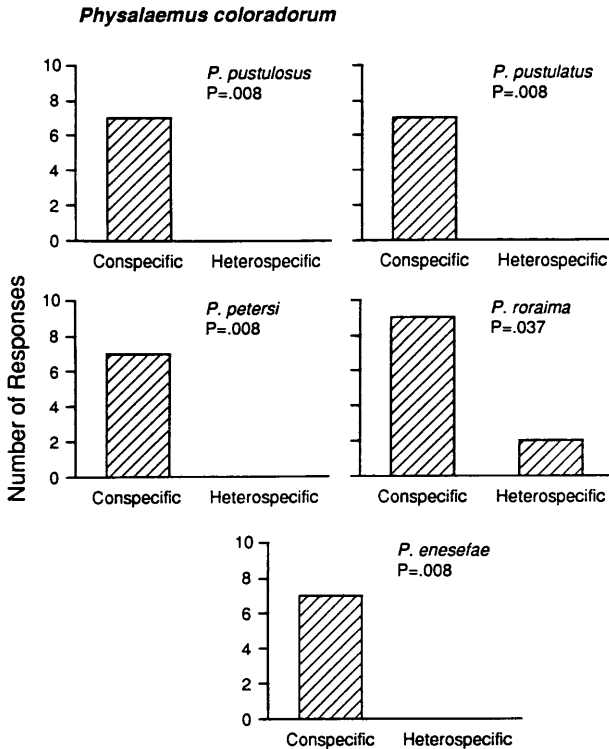
Physalaemus coloradorum

Figure 4 Phonotactic responses of female *Physalaemus coloradorum* to conspecific versus heterospecific calls.

significant, but the trend suggests a symmetry in efficacy of heterospecific signals between *P. pustulosus* and *P. coloradorum*.

Intraspecific call preferences

Male *P. pustulosus* add chucks to the whine component to increase the attractiveness of the call to females (Ryan, 1985). Chucks appear to be absent in other species of *Physalaemus* with the exception of some populations of *P. petersi*. We asked if female *P. coloradorum* would prefer chucks if they were to evolve. To do this we gave females a choice between a normal conspecific call and the same call to which three chucks from a *P. pustulosus* call were added (Fig. 7). Females showed a significant preference for the call with chucks. The preference for the chucks exhibited by the female *P. coloradorum* (9 v. 2) was not significantly different from the preference for chucks exhibited by the female *P. pustulosus* (19 v. 1) for their own calls with and without chucks ($G=1.34$, $P=0.25$; Ryan & Rand, 1990).

In response to vocalizations of other conspecific males *P. coloradorum* males produce calls in doublets or triplets with short inter-call intervals, usually less than 100 ms. Female *P. coloradorum* were given a choice between single and double calls. There was not a significant preference for the double calls (Fig. 8). However, the sample size is small and the trend is in the direction of preference for double calls. Male *P. pustulosus* do not produce calls in quick succession. Nevertheless, we
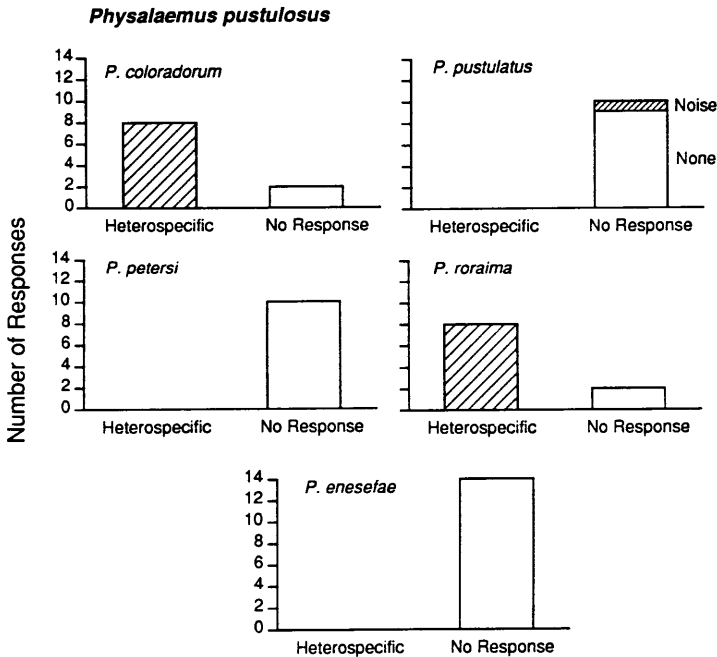
Figure 5 Phonotactic responses of female *Physalaemus pustulosus* to heterospecific calls versus white noise. A 'no response' is when females either respond to the noise or they show no phonotactic response in this test but show such a response in a subsequent test (see text for details).

asked if female *P. pustulosus* would prefer double calls to single calls if their males were to produce them. Females showed a significant preference for double calls (Fig. 8). Although this same preference exhibited by female *P. coloradorum* was not statistically significant, there was no significant difference between the females of each species in response to single and double calls ($G=1.98$, $P=0.16$).

DISCUSSION

Interspecific call preferences

The current geographic ranges of members of the *Physalaemus pustulosus* group and its two close relatives, *P.* 'roraima' and *P. enesefae*, are allopatric (with the exception of *P. pustulosus* and *P. enesefae*), and thus leads us to suggest that there has been no opportunity for character displacement or reinforcement between any pair of sister taxa. Nevertheless, females of *P. pustulosus* and *P. coloradorum* exhibit a strong preference for calls of conspecifics over those of heterospecifics. In this case the divergence of mate recognition systems during allopatry is sufficient to promote species-specific mate preferences in the absence of reinforcement fine-tuning such responses. These results support a widely held belief that the divergence of behaviours that cause reproductive isolation could result as an epiphenomenon of genetic
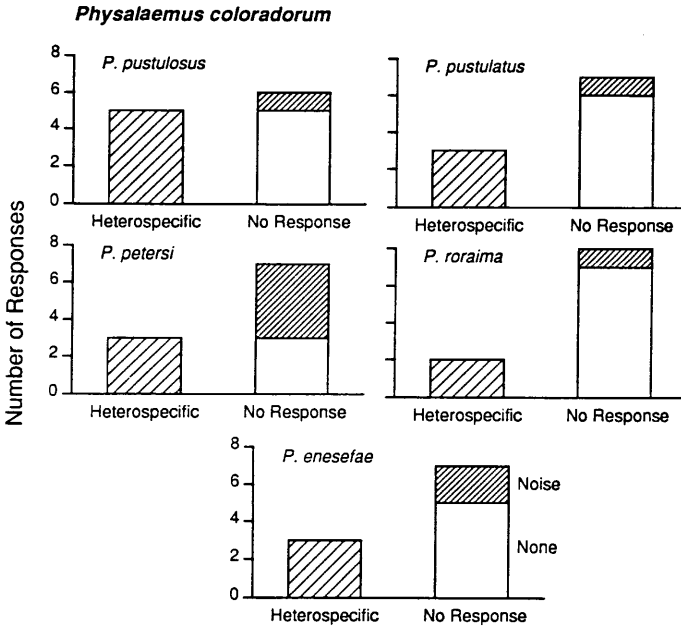
Physalaemus coloradorum

Figure 6 Phonotactic responses of female *Physalaemus coloradorum* to heterospecific calls versus white noise. A 'no response' is when females either respond to the noise or they show no phonotactic response in this test but show such a response in a subsequent test (see text for details).
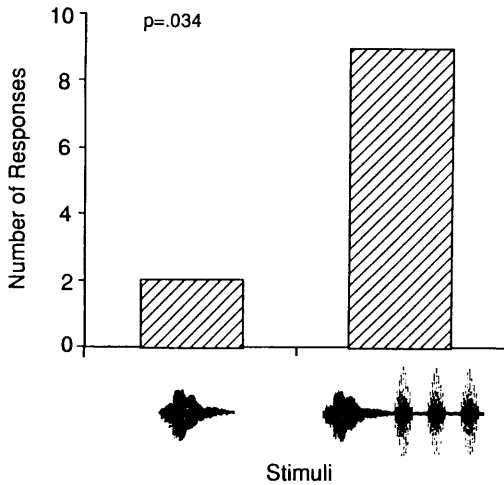

Figure 7 Phonotactic responses of female *Physalaemus coloradorum* to the normal, conspecific advertisement call and the same call to which three chucks of a *P. pustulosus* call have been added (calls represented in oscillograms).
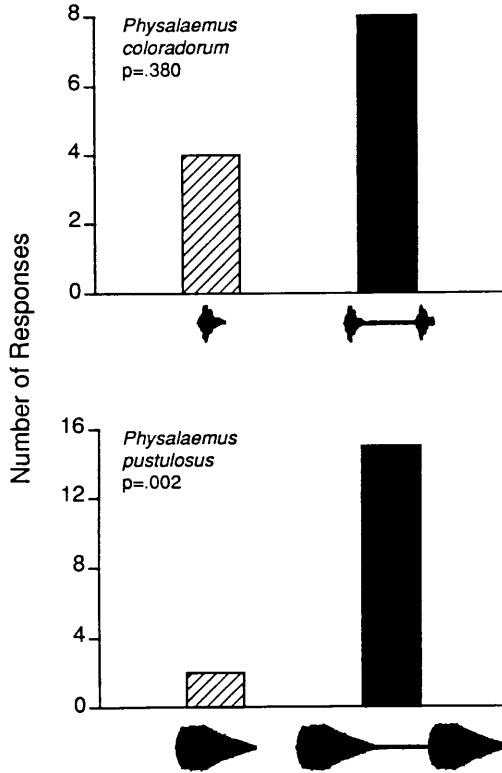
Figure 8 Phonotactic responses of female *Physalaemus coloradorum* and *P. pustulosus* to their own advertisement call presented either as a single or as a double call (calls represented in oscillograms).

divergence of allopatrically isolated gene pools (Darwin, 1859; Mayr, 1950, 1988; Paterson, 1985), as opposed to the theory that reinforcement of these mechanisms during secondary contact is crucial (Dobzhansky, 1937).

The species we tested can discriminate between conspecific and heterospecific calls, but another question asks if the heterospecific call is a viable communication signal. Ryan & Rand (in press) have discussed this issue in detail, and that discussion is summarized here.

Figure 9 illustrates various hypothetical relationships between a conspecific signal and the female preference function in univariate space, and emphasizes that discrimination between conspecific and heterospecific signals could result from several different relationships.

The preference functions a-d illustrated in Fig. 9 would result in female preference for the conspecific relative to the heterospecific signals illustrated, but how they would influence preferences among conspecifics and responses to heterospecific signals differ. Functions a–c (Fig. 9) 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. We do not know of any cases that would suggest function a (Fig. 9); this is probably because many studies concentrate either on species recognition or on sexual selection, but usually not both. For example, in our study the majority of experiments reveal
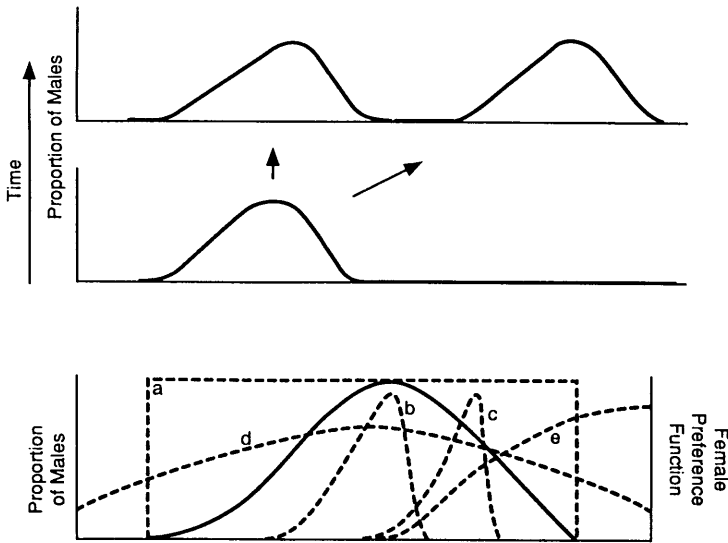
Figure 9 Top: Hypothetical distribution of species recognition signals in univariate space, illustrating the divergence of these signals in two populations during the process of speciation. Bottom: Solid line is the univariate distribution of male signals, and the dashed lines are various female preference functions relative to the male signal.

preference for conspecific signals and no response to heterospecifics. This would fulfil one of the predictions of the functions a–c (Fig. 9), but would not allow us to discriminate among those functions. There are several examples of the relationship illustrated by functions b and c (Fig. 9). For example, Gerhardt (1991) reviews call preferences in gray treefrogs, *Hyla versicolor*, and shows that preferences tend to generate stabilizing selection on some call properties and directional selection on others. Ryan & Keddy-Hector (1992) review numerous cases of directional female preferences for male courtship signals.

Function d (Fig. 9) predicts 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* (and possibly *P. coloradorum*) to heterospecifics are examples of such a phenomenon. Finally, function e (Fig. 9) predicts that females would respond to the conspecific signal but would prefer the heterospecific signal. Ryan & Wagner (1987) showed that female swordtails *Xiphophorus pygmaeus* preferred heterospecific males, *X. nigrensis*, to their own males. A similar example might be seen in this study. *P. coloradorum* females prefer their own calls to which a heterospecific signal has been added, to their own calls without such a signal. Also, female *P. pustulosus* prefer double calls to single calls, which is heterospecific rather than a conspecific manner of grouping calls. In both of these examples the difference in signals is presence/absence rather than a quantitative difference, as suggested in Fig. 9. Nevertheless, this is qualitatively the same phenomenon.

The relationship between signal and receiver properties has two important implications for understanding the evolution of communication systems. First, it tells us about the possible evolutionary patterns and prospects of signal–receiver evolution. For example: Are signal and receiver of the same species tightly matched, and different in all aspects from all other species, suggesting lock-step co-evolution? Are preferences

fairly broad, suggesting the retention of ancestral features, or perhaps convergence, in addition to the derived features that must be responsible for conspecific preferences? Do these preferences exhibit sufficient latitude to suggest various signals not exhibited by the species would be integrated into the communication system if they were to evolve (also see below)?

These considerations also affect some more philosophical issues of species concept. Paterson (1985) suggests that a species is a set of individuals sharing a common mate recognition system, and suggests that mate recognition, i.e. a positive response to another individual, and not discrimination among individuals, is the diagnostic feature in his definition: "The response of one mating partner to a signal from the other is here regarded as an act of recognition. Recognition is thus a specific response by one partner to a specific signal of the other ... I strongly emphasize that I imply no act of judgement and no act of choice on the part of the responding partner." It is not clear how responses to heterospecifics can be integrated into Paterson's species definition; perhaps that definition would merely classify these taxa as conspecific.

If taxa have evolved (derived) characters that result in species-specific preferences, why is it that in some cases heterospecific signals are recognized? This suggests the communication systems of the two species either have converged in certain characters or, perhaps more parsimoniously, that they share ancestral characters that suffice in eliciting mate recognition. Our experiments show that there are cases in which heterospecific signals can attract females. *P. pustulosus* females were attracted to calls of both *P. coloradorum* and *P.* 'roraima', and *P. coloradorum* females showed a tendency to be attracted to calls of *P. pustulosus*.

It is difficult to speculate as to the specific call and preference parameters that cause females to respond to one heterospecific call but not another. Some calls are more similar in spectral properties (e.g. *P. pustulosus* and *P. coloradorum*) while others are more similar in temporal properties (e.g. *P. pustulosus* and *P. enesefae*). Also, we cannot assume either that all properties of the call are attended to by females, or that the degree of difference in one domain (e.g. spectral) would have the same influence on preferences as the same degree in another domain (e.g. temporal). To understand fully the mechanism and evolution of these mate recognition systems, which include both the signals and the receivers, we need to combine a detailed quantitative analysis of calls with a detailed determination of the females' preference functions across all axes of call variation for all species under consideration.

Our first set of experiments, which show that females prefer conspecific to heterospecific calls, is consistent with many studies of species-specific mate recognition systems. By itself, these experiments could suggest that preferences and traits are closely matched systems that have co-evolved in a fine-tuned manner. However, the fact that the call of one species can elicit a response from more than one species suggests this need not be the case. Instead, it seems that females of some species share some parameters of the recognition system. Since many of these species are closely related, it seems probable that these common features are shared through common descent, although convergence is also a possibility that cannot be rejected without rigorous outgroup comparisons. The efficacy of these shared, and perhaps ancestral, characters shows that distant evolutionary history of a lineage influences its communication system, and that mate recognition might not be performed totally in the domain of recently derived characters.

Intraspecific call preferences

In *P. pustulosus* females prefer calls to which chucks have been added. Although male *P. coloradorum* do not add chucks, these females prefer calls to which chucks are added artificially. Thus in *P. coloradorum* the response of the receiver can be elicited by signals that are not part of the communication system. If our interpretation of the evolutionary history of the chuck is correct, this also suggests that the chuck evolved after the divergence of the *P. pustulosus–P. petersi* and *P. coloradorum–P. pustulatus* lineages, and leads us to conclude that the preference for chucks in both *P. pustulosus* and *P. coloradorum* might be shared through a common ancestor and thus existed prior to the evolution of the chuck. This would support the notion of sensory exploitation, which states that males can evolve traits to exploit pre-existing female preferences (Ryan, 1990a; Ryan & Rand, 1990; Ryan *et al.*, 1990).

Responses to single and double calls reflect a similar pattern to preferences for chucks; female *P. pustulosus* show a strong preference for a trait exhibited by a closely related species but lacking in their own. In this case, it is not clear if the double call is a derived or an ancestral condition relative to the species group. Relative to the other species in its group, male *P. pustulosus* have much larger vocal sacs and appear to use more air during calling. Dudley & Rand (1991) showed that the time needed for the vocal sac to deflate was *c* 250 ms, while the intercall interval of the double calls of *P. coloradorum* was about 170 ms. It is possible that the use of a larger air reservoir for calling, and the concomitant increase in vocal sac size and vocal sac deflation time, precludes the ability to produce calls in quick succession. Nevertheless, our experiments show that female *P. pustulosus* exhibit a preference for a trait not produced by their males, a preference which could favour this trait if it were to evolve.

In preference for both calls with chucks and for double calls, there is no significant difference in the degree of the preference between species in which the trait is present and in which the trait is absent. This rejects the hypothesis that the preference has been subjected to further evolution due to the presence of the male trait. However, our sample sizes are too small to give much confidence in accepting the null hypothesis of no difference. The hypothesis of trait elaboration after sensory exploitation has been recently supported by studies of preference for song repertoire in oscine birds. Searcy (1992) has shown that female grackles prefer repertoires to single song types, despite the fact that male grackles only produce the latter. Searcy also showed that among oscines, the strength of the preference is positively correlated with repertoire size. This suggests that there is a pre-exisiting preference for repertoires but that the strength of this preference is further elaborated in species exhibiting repertoires.

Our results on intraspecific mate recognition also illuminate the importance of ancestral properties of the females' preference. This is especially pertinent to studies in sexual selection. A controversial question has been why females exhibit preferences for male secondary sexual characters in species in which mate choice has no immediate effect on female reproductive success. Two hypotheses that have received much attention are Fisher's theory of runaway sexual selection (Fisher, 1958) and various hypotheses based on 'good genes' (e.g. Zahavi, 1975; Hamilton & Zuk, 1982; Kodric-Brown & Brown, 1984). Both of these hypotheses suggest that the female trait evolves under indirect selection (Kirkpatrick & Ryan, 1991). In these models, female

preferences are genetically correlated with male traits; the traits are under direct selection and the preferences co-evolve as correlated responses to the evolution of traits. Pre-existing preferences suggest that the male trait evolved after the preference. Thus models invoking the correlated co-evolution of traits and preferences can be rejected, and pre-existing preferences instead support the hypothesis of sensory exploitation – males evolve traits to exploit pre-existing preferences. Various forces inside and outside of the context of mate choice could be responsible for pre-existing preferences or for the further elaboration of the preference (Ryan, 1990a).

SUMMARY

Our results show that current mate recognition systems are sufficient for species-specific recognition among closely related species that are thought to have diverged in allopatry. This highlights the importance of derived characters in the mate recognition system. However, females of some species respond to heterospecific calls, suggesting the ancestral characters also can result in effective communication between the sexes.

We also examine traits that might be under sexual selection because they enhance the attractiveness of males relative to other conspecific males. *P. pustulosus* does this by adding chucks and *P. coloradorum* might do this by producing calls in doublets and triplets. Despite the fact that *P. pustulosus* does not produce double calls and that *P. coloradorum* does not produce chucks, the respective females prefer the trait that is lacking in their own males. This further emphasizes the importance of ancestral traits, in this case pre-existing female preferences.

Many studies have concentrated on how current, species-specific mate recognition systems ensure species integrity. Although our results do not refute this claim, we suggest that a view of the signals and receivers in mate recognition systems as constellations of derived and ancestral traits will yield a better understanding of communication between the sexes, whether among or within species.

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