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Signals, Species, and Sexual Selection

Michael J. Ryan

Many species of animals, especially birds and frogs, are readily identifiable to human observers by their distinctive visual and acoustical displays. These displays often characterize males that are attracting and courting females. Females rely on such species-specific displays to identify males; in particular, their concern is whether the males are conspecific or heterospecific, that is, members of their own or another species. Because heterospecific matings rarely yield viable offspring, it is important for females to recognize males of their own species, lest they waste a considerable investment in producing eggs.

The process of speciation involves a decrease in reproductive interactions and therefore a decrease in genetic exchange among populations. Because evolutionary change is more likely to occur in small groups of individuals, speciation enhances the probability of evolution. The understanding of how reproductive isolation evolves has therefore been a cornerstone of evolutionary biology. Reproductive isolation can result from the geographical isolation of taxa, but geographic barriers do not persist indefinitely. Reproductive isolation can also be maintained by behavioral differences, especially by differences in mate-recognition systems, which involve both the male's display and the female's preference for the display. Studies of the role of mate-recognition systems in promoting the integrity of species represent perhaps the main contribution of the field of animal behavior to the modern synthesis of evolutionary biology (Mayr 1982).

Many studies have documented a species-recognition function for male courtship. For example, Blair (1964) and his colleagues showed that female frogs are more likely to be attracted to a conspecific advertisement call than to a heterospecific call. The sensory basis of this mate-recognition system has been identified. Capranica (1976) and his colleagues demonstrated that the frog's auditory system is biased or "tuned" so that a conspecific call is more likely to elicit a neural response than is a heterospecific call.

Studies of mate recognition in frogs and fish reveal preferences for individuals, populations, and even members of closely related species

Because of the importance of species-specific courtship signals in species isolation, and the success with which the function of these signals has been identified, there has been a tendency to ignore variations of courtship signals within species. However, a renewed interest in sexual selection has led to the finding that variations in these signals among conspecific males influence the male's ability to acquire mates (Campbell 1972). It is now clear that mate-recognition systems not only result in conspecific mating preferences, but also influence preferences of mates within and between populations of the same species, and in some very unusual cases they even generate heterospecific mate preferences.

Mate preference in túngara frogs

The túngara frog, *Physalaemus pustulosus*, is unusual among frogs because of its complex advertisement call (Fig. 1). This call consists of a "whine" that is followed by up to six "chucks." The whine is fairly tonal, and decreases from a starting frequency of 900 Hz to a final frequency of 400 Hz in about 400 msec. The chuck is much briefer—only 30 msec—and has a much richer spectrum of frequencies. A typical chuck has a fundamental frequency of 220 Hz and 15 harmonics of that frequency. Especially when calling in isolation, a male tends to produce simple calls—a whine and no chuck. In a large chorus, however, the calls are complex and include both whines and chucks (Rand and Ryan 1981). This vocal system was first studied by A. Stanley Rand of the Smithsonian Tropical Research Institute in Panama. Rand and I have been collaborating on studies of these frogs for the past decade.

We have discovered that if a male hears calls broadcast from a tape recorder, he adds chucks to his own calls. He tends to add more chucks to his calls in response to chucks added to the broadcast calls (Rand and Ryan 1981). This response to vocal competition appears to be the reason that most males in large choruses produce complex calls.

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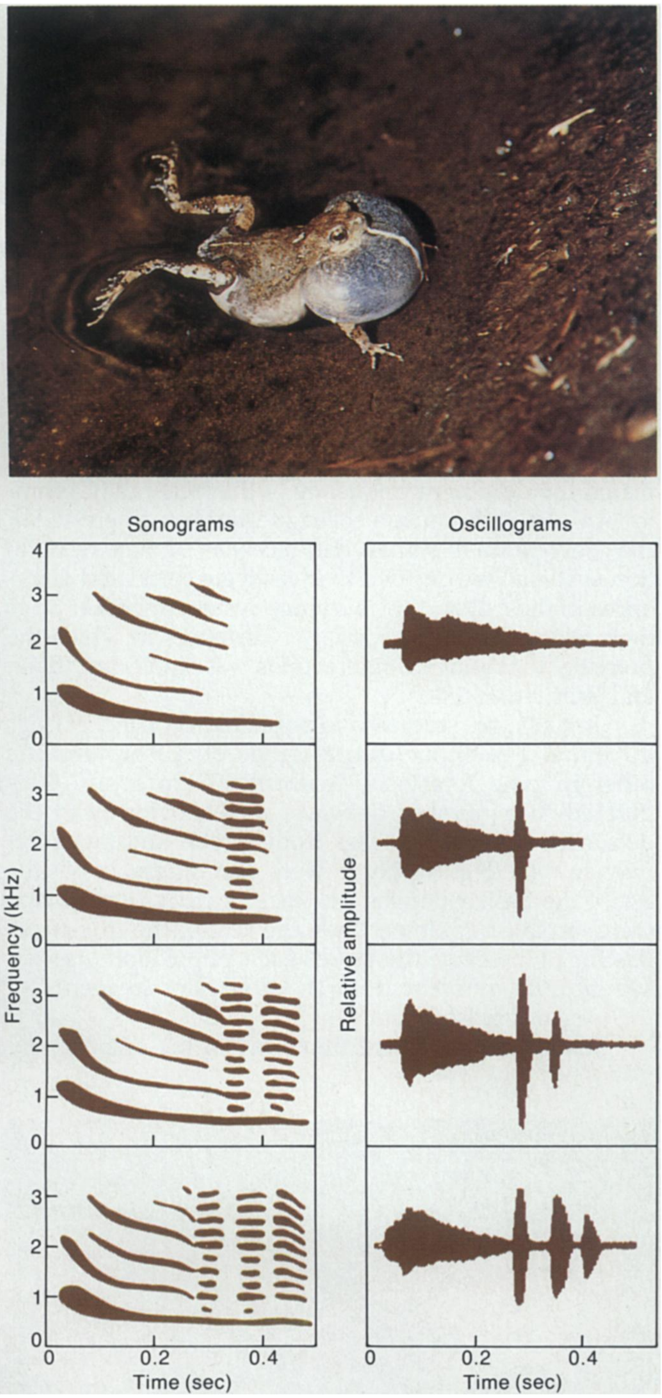

Figure 1. The mating call of the male túngara frog, *Physalaemus pustulosus*, comprises combinations of a "whine" and a number of "chucks." The whine is necessary and sufficient to attract the female; however, when competitors are present, the male adds chucks to his call. Sonograms and oscillograms reveal the structures of a simple call containing only a whine *(top graphs)* and more complex calls containing chucks *(proceeding down).*

Experiments in female phonotaxis suggest the advantages of complexity in male calls. A female is attracted to a speaker producing a simple whine. If the frequency structure of the whine is changed, however, the female is not attracted. Furthermore, if the whine is removed from a complex call, leaving only chucks, the female ceases to exhibit phonotaxis. The whine is therefore both necessary and sufficient for species recognition by the female (Ryan 1983a). In addition, given a choice between calls with and without chucks, the female prefers the call with chucks. Therefore males enhance their attractiveness to females by increasing the complexity of calls. Females rely on the whine to discriminate among species and use the chuck to discriminate among individuals within the species.

In measuring the mating success of male túngara frogs during two breeding seasons, I found that females were more likely to mate with larger males—both on a nightly basis and throughout the season. As a frog increases in size, so do his vocal cords, and because more massive vocal cords vibrate more slowly, larger frogs tend to have lower-pitched calls. This is true both among and within species. I tested the hypothesis that the greater mating success of larger males results from the preference of females for lower-frequency calls by conducting phonotaxis experiments using synthetic calls in which the whines were identical but the chucks had different frequencies. The experiments demonstrated that females prefer calls with chucks of lower frequency, suggesting that at least some of the mating advantage of larger males accrues from this female preference (Ryan 1980, 1983b).

These results, however, suggested a paradox. If females prefer calls with chucks, why do males bother to produce simple calls? There must be a cost involved; perhaps males conserve energy by producing complex calls only in the face of vocal competition. Some colleagues and I measured the increase in the rate of oxygen consumption in calling frogs. We found that calling is indeed energetically expensive; during calling, the rate of oxygen consumption increased fourfold to fivefold (Bucher et al. 1982). A very small increase in lactic acid suggested that it is primarily aerobic metabolism that supports calling behavior (Ryan et al. 1983). However, no difference between the energy used to produce a complex call and the energy used to produce a simple call was observed.

There is another potential cost in calling: not only do calls attract females, they can also attract predators. In fact, Marler (1955) suggested that pressures of predation have led to the convergence of structure and function in bird calls. Tuttle and I conducted a series of studies on the frog-eating bat, *Trachops cirrhosus*, which locates prey by orienting to the frog's advertisement call (Tuttle and Ryan 1981)(Fig. 2). Like female túngara frogs, frog-eating bats are attracted to a simple call, and when given a choice between a simple and a complex call, they too prefer the call with chucks (Ryan et al. 1982). The ability of the male túngara frog to vary the number of chucks in his call allows him to balance this cost of predation with the benefit of mate attraction.

The two functions of courtship display in the túngara frog probably evolved in response to different selection forces. The whine, used for species recognition, evolved under selection forces associated with the advantages of conspecific relative to heterospecific matings. The female preference for calls with chucks, and especially chucks with lower frequencies, evolved under the influence of sexual selection generated by female choice and the countervailing selection force of predation.

Mate preference in cricket frogs

The mate recognition system consists of not only the signal but also the receiver. Variations in signals have been more extensively documented than variations in receivers because signals are more accessible to the researcher. It is much easier to compare the colors and calls of different species than to compare the properties of the visual and auditory systems that decode those stimuli.

Anurans have emerged as a model system in the study of communication for a number of reasons (Wilczynski and Ryan 1988). The male frog's call is relatively simple compared to bird song, and therefore it can be more easily quantified and synthesized. Also, female frogs readily exhibit phonotaxis in response to broadcasts of natural or synthetic calls, allowing experimental determination of the importance of various parameters. Another important advantage, perhaps unique to frogs among all vertebrates, is the detailed understanding of the properties of the auditory system responsible for decoding the conspecific advertisement call. This allows for the investigation of both aspects of the mate recognition system: the signal and receiver.

Unlike other vertebrates, amphibians have two organs in the inner ear that are stimulated by airborne sound: the amphibian papilla and the basilar papilla. Each papilla is enervated by fibers from the eighth cranial nerve. These two organs differ in several ways, one being their sensitivity to frequencies. The nerve fibers emanating from the amphibian papilla tend to be most sensitive to lower frequencies, usually below 1,500 Hz, whereas the fibers that enervate the basilar papilla are tuned to higher frequencies, usually above 1,500 Hz. The frequency to which each inner ear organ is most sensitive—called the best excitatory frequency (BEF)—is usually matched to the more energetic frequencies of the advertisement call. For example, the advertisement calls of the bullfrog and the green treefrog have two concentrations of spectral energy; one of these is matched by the BEF of the amphibian papilla and the other by the BEF of the basilar papilla (Zakon and Wilczynski 1988). Not all calls stimulate both inner ear organs. For example, the whine of the túngara frog stimulates primarily the amphibian papilla (Ryan et al., in press.).

The call of the cricket frog *(Acris crepitans)* sounds like a loud click, and these clicks are organized into complex call groups. The call has a dominant frequency of 2,800 to 4,100 Hz, and stimulates primarily the basilar papilla. Nevo and Capranica (1985) documented considerable call variation in this species across its range in North America. They also showed that between two populations separated by 2,500 km, there were differences in the tuning of the auditory system that tended to match the dominant frequency of the local call (Capranica et al. 1973). Because a colleague and I are interested in the coevolution of signals and receivers of mate recognition systems, we decided to investigate correlated differences in the call and the auditory system in cricket frogs over relatively small geographic distances in which the potential for biological interactions was significant (Ryan and Wilczynski 1988).

Initially, we studied two populations of cricket frogs in central Texas; one in grasslands of Austin, and the other in pine forests of Bastrop, 65 km away. Calls differed in a number of ways, most obviously in the dominant frequency—frogs from Austin had lower-frequency calls (Fig. 3). There were also differences in the BEF of the basilar papilla. The BEFs of frogs from Austin were, on average, lower than the BEFs of the frogs from Bastrop. However, the BEF of each population was not significantly different from the dominant frequency of the local advertisement call.

Just as the dominant frequency of the call can vary

Figure 2. In addition to attracting a female frog, the call of the male túngara frog can attract the frog-eating bat, *Trachops cirrhosus*. The bat responds to complexities in the frog's call in much the same way that the female frog does. In the photograph above a bat feeds on a male túngara frog that had been calling. (Photo by M. Tuttle.)

with body size, so too can the BEF of the basilar papilla. Several authors have suggested that congruence between the signal and receiver of a mate recognition system can be maintained by incidental effects of body size (Passmore 1981; Paterson 1982). For example, selection might favor larger body size in a population living in a drier habitat because of its advantage in minimizing desiccation rates. If so, the mate recognition systems of this population and a population living in a wetter habitat would diverge while remaining congruent within each population. The larger frogs would have lower-frequency calls and lower BEFs as a result of correlated responses of the signal and receiver to selection on body size, despite any direct selection on the communication system. These differences might even result in frogs from the different populations that do not recognize each other as potential mates. Nevo and Capranica (1985) made such a suggestion in order to explain the correlated variation in calls and tuning of the two populations of cricket frogs they studied (Capranica et al. 1973).

The frogs from Austin and Bastrop that we studied differed in body size: the Austin frogs were bigger and, as expected, had calls with lower dominant frequencies and basilar papillae with lower BEFs. However, size did not explain differences in the signals and receivers. An analysis of covariance showed that even after adjusting for differences in body size, call frequencies and BEFs differed between populations but not within each population.

We considered whether these population differences in the mate recognition system are biologically meaningful. If frogs from these two populations were to come into contact, would females prefer local males over males from the other population? We created call groups representing the two populations that were identical in the number of calls and call repetition rate, and found that females from Austin preferred the local calls. We also constructed synthetic calls that were identical in all aspects except dominant frequency. Again, females from Austin exhibited a significant preference for the local call.

Although like most frogs, cricket frogs have an advertisement call that results in females preferring males of their species rather than heterospecific males (Nevo and Capranica 1985), there is variation in both the signal and the receiver between populations of different species. This variation, which is not attributable to differences in body size alone, could generate mate preferences among populations.

Our study in some ways parallels research on bird dialects. Those studies have shown that there are significant and abrupt differences in the songs of conspecific birds from neighboring populations. Researchers have suggested that this variation, coupled with female mate preference, could result in genetic structuring of populations; that is, matings would be more likely to occur within than between call variants (Baker and Cunningham 1985). This idea is controversial because of the difficulties of conducting female phonotaxis experiments with birds and characterizing the sensory basis of the female preference (Andrew 1985). Our studies of cricket frogs, however, suggest that variations in the conspecific advertisement call between geographically close populations could lead to local mate preferences and possibly to genetic differentiation among populations.

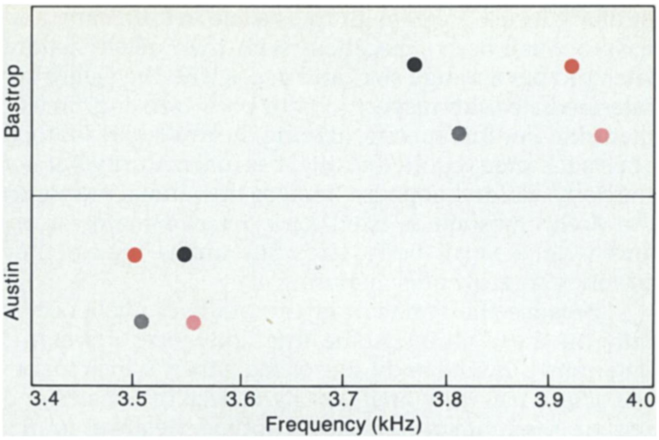

Figure 3. Differences in the calls of identical species from different geographical regions can be significant. Shown above are the average dominant frequencies of calls *(black dots)* and the best excitatory frequencies of the basilar papilla *(red dots)* for cricket frogs from two areas in Texas, Austin and Bastrop. The dots with lighter shading represent the data after being adjusted for differences in body size.

Heterospecific mate preference

The selection of mates is usually hierarchical. Among conspecific males, choice, or sexual selection, usually proceeds only within the constraints of species recognition. This is exemplified by the mate-recognition systems discussed above. A female túngara frog relies on the whine of the male to select the correct species, and then proceeds to discriminate among conspecifics using the male's chuck. However, species-specific courtship signals do not always result in conspecific mate preferences. Two species of insects of the genus *Drosophila* exhibit mating asymmetries. The females of one species of this pair of sister species demonstrate conspecific mate preference, while the females of the other species mate randomly with males of either species (Kaneshiro 1980). Similar results have been reported for fish of the genera *Gasterosteus* (McPhail 1969; Moodie 1982) and *Trichogaster* (McKinnon and Liley 1987).

Our studies of fish of the genus *Xiphophorus*, which includes the platys and swordtails (Fig. 4), suggest that sexual selection for large body size can result in females of one species preferring to mate with males of another species. Larger males of many species have greater mating success, either because they are better able to compete for access to females or, as in the case of túngara frogs, because females prefer larger males. In most of these species, it is not clear whether differences in body size are the result of environmental effects or genetic differences. Because evolution proceeds only in the presence of genetic variation, this lack of knowledge is not trivial.

Swordtails and platys are unusual in that much of the variation in body size is attributable to allelic variation at a single Y-linked locus, the pituitary locus (Kallman 1984). This locus controls the timing of sexual maturity. Because males in this genus cease to grow upon reaching sexual maturity, this locus also influences body size. In the swordtail, *X. nigrensis*, from the Rio Choy in Mexico, males can have one of three alleles at the Y-linked pituitary locus. Males with the *s* allele mature early and have a small body size, those with the *L* allele mature later and have a large size, and males with the *I* allele are intermediate with respect to both body size and time to maturity. For this species, altering the availability of food affects the time required to attain sexual maturity but not the body size at that point. Because the pituitary locus on the X chromosome is fixed for *s*, females mature early and with a small body size, but unlike males, they continue to grow after maturing.

Because the variation at the pituitary allele occurs only on the Y chromosome, the body size of a son is determined by the body size of the father, which makes possible a paternity analysis. By collecting females and raising their offspring, the genotype (relative to the pituitary locus) is revealed. When these data are compared to the frequency distribution of the three genotypes in nature, the relative reproductive success of each pituitary allele can be determined. Because in our experiments the females were fertilized by males present at the time of sampling, much of the variance in reproductive success of the pituitary alleles was due to sexual selection—some combination of female choice and male competition.

Colleagues and I showed that small males were at a significant reproductive disadvantage; across generations there was a decrease in the *s* allele. Furthermore, some of this decreased reproductive success derived from female choice. Individual males of various sizes were placed at either end of a large aquarium, separated from a center section by glass partitions. A female was placed in the center, where she could consort with the male at either end. In most comparisons females spent significantly more time with the larger male (Ryan, et al., in press). Female preferences are therefore an important source of selection on male size, although the greater swimming endurance of larger males suggests a role for male competition in male reproductive success (Ryan 1988).

A study of male mating behavior in swordtails revealed striking differences correlated to male size. Larger males performed a conspicuous display of courtship, whereas smaller males did not attempt to court females (Ryan and Causey 1989) (Fig. 5). Instead, the smaller males chased after females, trying to force copulation—a difficult task when faced with internal fertilization and quickly retreating females. Within the intermediate-size class, it was also found that smaller males chased while larger males courted. The transition between chasing and courting occurred at a length of about 29 mm. The results of female choice tests coincided with these results; females usually discriminated among males if one male was shorter and one longer than 29 mm. No discrimination was observed when both males were on one side of this transition.

Unlike other studies, our study reveals that this selection favoring larger males results in changes in allelic frequencies across generations; that is, our study documents genetic evolution by sexual selection. *X. nigrensis* males that are preferred less adopt alternative mating behaviors, and to some extent, there is a correlation between genotype and mating behavior.

The closest relative of *X. nigrensis* is *X. pygmaeus*, found in the nearby Rio Axtla. All *X. pygmaeus* males are small, encompassing the size range of the small-size class and the smaller males of the intermediate-size class of *X. nigrenis*. Wagner and I wondered if the pituitary alleles responsible for large body size in *X. nigrensis* would be favored by sexual selection if they were to appear in the *X. pygmaeus* population. Is the female preference present in the absence of the male trait? This might be true if the preference were present in the common ancestor of *X. pygmaeus* and *X. nigrensis* and were not lost in *X. pygmaeus* after the two taxa diverged.

We presented female *X. pygmaeus* with a choice between an *X. pygmaeus* male and a large *X. nigrensis* male. There was a strong preference for the larger, heterospecific male. Noting that the male *X. nigrensis* possesses a well-developed sword, which is lacking in *X. pygmaeus*, we decided to remove the sword of the *X. nigrensis* male and repeat the experiments. Female *X. pygmaeus* still preferred the larger *X. nigrensis*. Surprisingly, the female *X. pygmaeus* preferred the heterospecific male when both males were 26 mm long. The heterospecific preference was extinguished only when both males were small and of the same size. Under those circumstances, females did not exhibit any preference. In all cases, female *X. nigrensis* preferred her own conspecifics over *X. pygmaeus* males (Ryan and Wagner 1987).

Figure 4. In experiments, the swordtail, *Xiphophorus nigrensis*, demonstrates a startling behavior: the female prefers a male of a closely related but different species if the heterospecific fish is larger than males of her own species. Shown here are a male *(top)* and female of the species. (Photo by H. R. Axelrod.)

Differences in body size alone cannot explain the asymmetric mating preferences observed. Behavior seems to be important as well. Franck (1964) reported that male *X. pygmaeus* lacks the display that characterizes the courtship behavior of its sister species and many other swordtails. Causey and I reconfirmed this, and showed that male *X. pygmaeus* behave toward females as do small male *X. nigrensis*—chasing the females in attempts to force copulation. In most of the *X. nigrensis*–*X. pygmaeus* pairs tested, heterospecific males were not only larger, they also possessed the characteristic courtship display. Only when both males were small, and both lacked the display, did the heterospecific preference cease to occur. The preference for the 26-mm heterospecific male is nevertheless confusing—*X. nigrensis* males of this size usually do not court.

It is not clear why the mating behavior of an entire species consists of what is considered alternative behavior. Courtship behavior is clearly favored by sexual selection through female choice in *X. nigrensis*, and it appears as if it might be favored if it were to evolve in *X. pygmaeus*. Obvious hypotheses, such as increased predation on courting males, have yet to be tested. Other possibilities such as phylogenetic influences and genetic constraints are being investigated. The preference for large, courting males in female *X. pygmaeus* and the lack of such a trait in their male counterparts has led to an interesting situation in which sexual selection can override considerations of species recognition. These species do not occur together in nature, but they do hybridize in the laboratory. If they were to come into contact, sexual selection could cause gene pools of the two species to merge. Furthermore, the study suggests that in some cases the female's preference, although not expressed, is "waiting" to be exploited by males with certain traits. Andersson (1982) has made a similar interpretation as a result of his study of female preference for long tails in widow birds; females preferred males with tails that were artificially lengthened beyond the maximum length exhibited by the species.

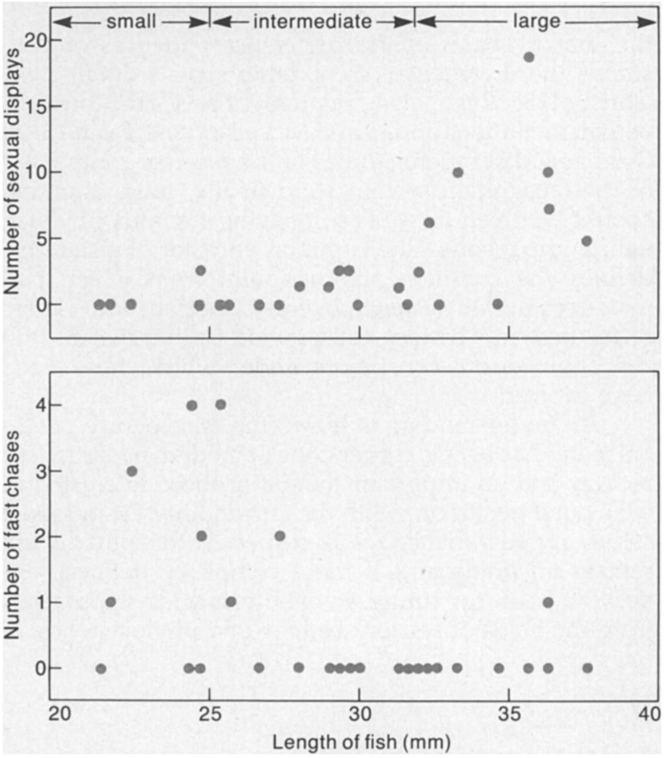

Figure 5. In the presence of females, large *X. nigrensis* males engage in courtship displays, whereas smaller *X. nigrensis* males simply chase the females. This may be related to the tendency of females to be attracted to larger males.

Evolution of mate recognition

There is little debate that mate-recognition systems effect mating between conspecifics. However, there is disagreement over the factors involved in the evolution of these systems. The disagreement highlights the important distinction between the evolved function of a trait and its incidental effects (Williams 1966; Gould and Vrba 1982). The function, in a strict sense, is that initial effect for which selection favored the trait. An extreme example of an effect not favored by selection is the attraction of bats to the chuck of male túngara frogs.

Dobzhansky (1937) suggested that mate-recognition systems evolved to serve the function of species isolation. This suggests the function is negative—one of avoidance. Paterson (1982) criticized this thesis because it viewed the species as an adaptive mechanism. He argued instead for the positive effects, suggesting that mate-recognition systems evolved to promote mating between individuals of similar genotypes (conspecifics).

Dobzhansky and Paterson both emphasized strong stabilizing selection on male courtship signals, and they tended to discount the significance of intraspecific variation. The studies reviewed here have suggested that both views are too typological, regardless of whether the evolved function of mate-recognition systems is one of repulsion or attraction. Courtship signals vary among males in the same population (e.g., túngara frogs and swordtail fish), and among populations of the same species (e.g., cricket frogs). And this variation is biologically meaningful, being the target of sexual selection by female choice. At least for the chuck component of the túngara frog's call, there is ample phylogenetic evidence that the vocal structures that allow males to produce the chuck evolved under the influence of sexual selection and not species recognition (Ryan 1985). Finally, there is the example of *X. pygmaeus*, in which female preference for courtship and larger size, a clear example of sexual selection and not species recognition, overrides the consideration of mating with conspecifics and results in females preferring heterospecific males.

Species recognition might be an evolved function, but it might also be an incidental effect of male courtship signals. A number of factors can be responsible for the divergence of signals that result in conspecific mate recognition. I have given examples of the importance of sexual selection—a possibility discussed extensively by West-Eberhard (1979, 1983, 1984; also Lande 1981).

Studies of mate-recognition systems are now moving away from notions of typology and embracing the idea of the rich and diverse variation within species as an important biological phenomenon. Some studies have revealed considerable variation in preferences among conspecific females (Majerus et al. 1982; Breden and Stoner 1987; Houde 1988). Others have investigated how the sensory basis of the preference enhances or constrains the divergence of courtship signals (Ryan 1986; Christy 1988; Ryan, et al., in press) or biases the direction of their evolution (Endler and McLellan 1988; Ryan 1990). Still needed are more studies of the receiver component of the recognition system. And finally, more attention should be given to studies involving rigorous phylogenetic comparisons. The common ancestor of sister taxa defines the common starting point from which two mate-recognition systems diverged. Perhaps knowledge of the system's history will provide further insight into the phylogenetic constraints under which these traits have evolved.

An understanding of how females recognize potential mates has been a cornerstone of modern evolutionary biology and an important pursuit of those interested in behavioral evolution. With the current interest in sexual selection and variability within species, this pursuit will remain an important, if more complexly defined, endeavor. Look for future studies to include approaches from the fields of sensory biology and phylogenetics.

References

Andersson, M. 1982. Female choice selects for extreme tail length in widow birds. *Nature* 299:818–20.

Andrew, R. J. 1985. Questions about the evolution of bird song. *Behav. Brain Sci.* 8:100.

Baker, M. C., and M. A. Cunningham. 1985. The biology of bird song dialects. *Behav. Brain Sci.* 8:85–100.

Blair, W. F. 1964. Isolating mechanisms and interspecies interactions in anuran amphibians. *Quart. Rev. Biol.* 39:334–44.

Breden, F., and G. Stoner. 1987. Male predation risk determines female preferences in the Trinidad guppy. *Nature* 329:831–33.

Bucher, T. L., M. J. Ryan, and G. A. Bartholomew. 1982. Oxygen consumption during resting, calling, and nest building in the frog *Physalaemus pustulosus*. *Physiol. Zool.* 55:10–22.

Campbell, B., ed. 1972. *Sexual Selection and the Descent of Man, 1871–1971*. Aldine.

Capranica, R. R. 1976. Morphology and physiology of the auditory system. In *Frog Neurobiology*, ed. R. Llinas and W. Precht, pp. 552–75. Springer-Verlag.

Capranica, R. R., L. S. Frischkopf, and E. Nevo. 1973. Encoding of geographic dialects in the auditory system of the cricket frog. *Science* 182:1272–75.

Christy, J. H. 1988. Pillar function in the fiddler crab *Uca beebei* (II: Competitive courtship signalling). *Ethology* 78:113–28.

Dobzhansky, T. 1937. *Genetics and the Origin of Species*. Columbia Univ. Press.

Endler, J., and T. McLellan. 1988. The processes of evolution: Towards a newer synthesis. *Ann. Rev. Ecol. Syst.* 19:394–421.

Franck, D. 1964. Vergleichende an lebendgebarenden Zahnkarpfen der Gattung *Xiphophorus*. *Zoologisches Jahrbuch* 71S:117–70.

Gould, S. J., and E. Vrba. 1982. Exaptation—a missing term in the science of form. *Paleobiol.* 8:4–15.

Houde, A. 1988. Genetic differences in female choice between two guppy populations. *Animal Beh.* 36:510–16.

Kallman, K. D. 1984. A new look at sex determination in poeciliid fishes. In *Evolutionary Genetics of Fishes*, ed. B. Turner, pp. 95–171. Plenum.

Kaneshiro, K. Y. 1980. Sexual isolation, speciation and the direction of evolution. *Evolution* 34:437–44.

Lande, R. 1981. Models of speciation by sexual selection on polygenic characters. *Proc.* NAS 78:3721–25.

Marler, P. 1955. Characteristics of some animal calls. *Nature* 176:6–8.

Majerus, M. E. N., P. O'Donald, and J. Weir. 1982. Female mating preference is genetic. *Nature* 300:521–23.

Mayr, E. 1982. *The Growth of Biological Thought*. Harvard Univ. Press.

McKinnon, J. S., and N. R. Liley. 1987. Asymmetric species specificity in response to female sexual pheromone by males of two species of *Trichogaster* (Pisces:Belodontidae). *Can. J. Zool.* 65:1129–34.

McPhail, J. D. 1969. Predation and the evolution of a stickleback *(Gasterosteus)*. *Canadian Journal of the Fisheries Research Board* 26:3183–3208.

Moodie, G. E. E. 1982. Why asymmetric mating preferences may not show the direction of evolution. *Evolution* 36:1096–97.

Nevo, E., and R. R. Capranica. 1985. Evolutionary origin of ethological reproductive isolation in cricket frogs, *Acris*. *Evol. Biol.* 19:147–214.

Paterson, H. E. H. 1982. Perspectives on speciation by reinforcement. *So. Afr. J. Sci.* 78:53–7.

Passmore, N. 1981. The relevance of the specific mate recognition concept to anuran reproductive biology. *Monitore Zoologica Italiano* 6:93–108.

Rand, A. S., and M. J. Ryan. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Zeitschrift für Tierpsysiologie* 57:209–14.

Ryan, M. J. 1980. Female mate choice in a neotropical frog. *Science* 209:523–25.

———. 1983a. Frequency modulated calls and species recognition in a neotropical frog, *Physalaemus pustulosus*. *J. Comp. Physiol.* 150:217–21.

———. 1983b. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. *Evolution* 37:261–72.

———. 1985. *The Túngara Frog. A Study in Sexual Selection and Communication*. Univ. Chicago Press.

———. 1986. Neuroanatomy influences speciation rates among anurans. *Proc.* NAS *83:1379–82.*

———. 1988. Swimming endurance, genotype, and sexual selection in a swordtail *Xiphophorus nigrensis*. *Copeia* 1988:484–87.

———. In press. Sexual selection, sensory systems, and sensory exploitation. *Oxford Surv. Evol. Biol.*

Ryan, M. J., G. A Bartholomew, and A. S. Rand. 1983. Energetics of reproduction in a neotropical frog, *Physalaemus pustulosus*. *Ecology* 64:1452–62.

Ryan, M. J., and B. J. Causey. 1989. "Alternative" mating behavior in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus* (Pisces: Poeciliidae). *Beh. Ecol. Sociobiol.* 24:341–348

Ryan, M. J., J. Fox, W. Wilczynski, and A. S. Rand. In press. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*.

Ryan, M. J., D. K. Hews, and W. E. Wagner, Jr. In press. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. *Beh. Ecol. Sociobiol.*

Ryan, M. J., M. D. Tuttle, and A. S. Rand. 1982. Bat predation and sexual advertisement in a neotropical frog. *Am. Naturalist* 119:136–39.

Ryan, M. J., and W. E. Wagner, Jr. 1987. Asymmetries in mating preferences between species: Female swordtails prefer heterospecific mates. *Science* 236:595–97.

Ryan, M. J., and W. Wilczynski. 1988. Coevolution of sender and receiver: Effect on local mate preference in cricket frogs. *Science* 240:1786–88.

Tuttle, M. D., and M. J. Ryan. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science* 214:677–78.

West-Eberhard, M. J. 1979. Sexual selection, social competition, and evolution. *Proc. Am. Phil. Soc.* 123:222–34.

———. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* 58:155–83.

———. 1984. Sexual selection, competitive communication and species-specific signals in insects. In *Insect Communication*, ed. T. Lewis, pp. 283–324. Academic Press.

Wilczynski, W., and M. J. Ryan. 1988. The amphibian auditory system as a model for neurobiology, behavior and evolution. In *The Evolution of the Amphibian Auditory System*, ed. B. Fritzsch et al., pp. 3–12. Wiley.

Williams, G. C. 1966. *Adaptation and Natural Selection. A Critique of Some Current Thought*. Princeton Univ. Press.

Zakon, H., and W. Wilczynski. 1988. The physiology of the anuran eighth nerve. In *The Evolution of the Amphibian Auditory System*, ed. B. Fritzsch et al., pp. 125–55. Wiley.