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News Focus

26TH INTERNATIONAL ETHOLOGICAL CONFERENCE: Behaviorists Listen In as Animals Call and Croak

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BANGALORE, INDIA--Animal communication was a hot topic when 400 researchers from 39 nations gathered here at the 26th International Ethological Conference from 2 to 9 August. Some of the most vocal discussions explored how animals speak their minds, from calling in grasshoppers to croaking in frogs.

Female Frogs Join the Chorus

Although it may sound harsh to human ears, the croaking of frogs on a rainy spring night is actually the sound of romance. Male frogs are trying to capture the attention and admiration of females with long, loud calls--displays of stamina that are thought to showcase a male's fitness. Now an Indian researcher has found that the females, often thought to be silent partners in this serenade, take part in the concert as well.

Although a few studies have noted female calls, most research on frog communication has concentrated on the louder males, so that many researchers believed that female frogs had no voice at all, says frog communication expert Stanley Rand of the Smithsonian Tropical Research Institute in Gamboa, Panama. But Debjani Roy, a herpetologist working at the Institute of Self Organizing Systems and Biophysics at North Eastern Hill University in Shillong, India, has found that for three species of Indian frogs, the evening concert is a duet, in which females respond to the males with feeble calls that indicate their readiness to mate. "Roy's discovery throws a very different light on mate acquisition in these species," says Rand. "Females play

a more active role and are no longer passive partners in a system dominated by males."

Roy was doing a taxonomic survey of the frogs of northeastern India, analyzing frog calls as one way to distinguish the various species. Out of curiosity she and her colleagues analyzed both female and male behavior on their evening sojourns to ponds, where they often worked from 4:00 p.m. to 4:30 a.m., dodging rain, blood-sucking insects, and poisonous snakes. Roy first spotted the frogs visually using torches and kerosene lamps, which gave clues to their sex because females are much larger than males. Then she put microphones near the frogs to record their croaks, and watched and listened until they stopped calling sometime the next morning. Her long nights paid off: In three species--a tree frog, *Polypedates leucomystax*, a cricket frog, *Limnonectes limnocharis*, and the so-called skipper frog, *Euphylyctis cyanophlyctis*--she found that females croaked too, and the female call was "the catalyst" for the next step in courtship.

"The females respond to the male advertisement calls by producing feeble, low tonal calls to initiate courtship," she explains. In the case of the tree frog, for example, the female emerged and sat near the male that had started calling first, which was always among the largest males. When the male stopped calling, the female gave feeble croaks, apparently indicating that she had made her choice and was ready to mate. The male then began calling again, even more loudly. Finally, they mated.

Roy and her colleagues confirmed this behavior in the lab: When female tree frogs heard tapes of various males played through different speakers, they called after hearing the largest, heaviest males, and they moved toward that speaker. "Females do not mate randomly, but they are intelligent enough to weigh their benefits by mating with males whose calls contain more acoustical energy," explains Roy. Females are also sparing with their low-pitched, slow-paced calls; in a breeding group of females, Roy found that only those gravid with eggs gave the reciprocal call and were willing to mate. The rarity of female calls may be one reason why they weren't noted before. Although Roy recorded male calls on each of 148 nights of observation, she heard females' croaks on only 15 days.

Roy's discovery of a female call is "significant," says Peter M. Narins, a behavioral ecologist at the University of California, Los Angeles, who himself has studied vocalization in *P. leucomystax* but had never recorded a female's reciprocal call. Rand adds that Roy's study suggests that frog communication and courtship is much more complicated than had been

thought. Says Rand: "It now seems that males and females, at least in these few species, get into a conversation before they decide to mate."

Why Frogs and Insects Sing the Same Song

City dwellers seeking rural peace and quiet are often rudely surprised by the deafening croaks of a bullfrog chorus, not to mention the relentless drone of katydids and grasshoppers. Although wildly different in pitch, duration, and rhythm, all of these choruses have the same purpose: Males are passionately trying to attract mates. Now researchers studying the rhythm of male calls have noted another surprising similarity: Insects and frogs follow the same "rules" of calling. Females tune in to the male that leads the chorus, and males of each species have developed almost identical strategies for being the leader, behavioral ecologist Michael Greenfield reported at the meeting.

"What I find most remarkable is the similarity in mechanisms in both vertebrates and invertebrates," says Greenfield, who is at the University of Kansas, Lawrence. Such parallels in organisms separated by hundreds of millions of years of evolution, he says, "suggest remarkable levels of convergence in the mechanisms of collective behavior."

In both frogs and insects, males stay still and lure females with rhythmic calls. Females are most likely to respond to loud calls, which presumably indicate that the male is nearby and perhaps that he is vigorous. Researchers have also shown that when female frogs or grasshoppers hear calls of roughly similar loudness, they listen and orient only to the male that calls first, a so-called precedence effect. This may happen because it's easier for a female to locate the source of a signal if she tunes out any subsequent, competing calls, says Greenfield. From the male perspective, of course, this means that every male in the crowd wants to be first.

Now Greenfield and his colleague Stanley Rand of the Smithsonian Tropical Research Institute (STRI) in Gamboa, Panama, have shown that males in these very different species follow almost exactly the same path to that goal. When a male hears a neighbor's song, he postpones his next call until the neighbor stops, in what neuroethologists call an "inhibitory resetting" mechanism. The male restarts his own rhythmic calling slightly less than one period later, thus boosting his call into the lead. But in a crowd of croaking frogs or whining katydids, a male following this rule too closely would never sing. So theory suggests that males should pay attention to only a few of their noisy neighbors--those most likely to compete for nearby females--and

ignore the rest.

The researchers tested the calling patterns of two species of acridid grasshoppers and one species of frog, lugging sophisticated audio equipment and four loudspeakers into the field to simulate combinations of competing callers. The experiments confirmed what theory predicted--males of all three species paid attention to only some of their neighbors. And all used the same so-called sliding threshold rule: Pay attention to the loudest neighbor and all those whose calls are within 6 to 8 decibels of that neighbor. "The mechanisms controlling female response and male signal timing parallel one another" in frogs and insects, says Greenfield.

The researchers discovered other subtleties in the calling rules of the Panamanian tunganá frog when they studied it in STRI's Gamboa lab. These frogs modified the sliding threshold principle with a new rule: When several neighbors are all relatively loud, pay attention to the three loudest. But when the nearest neighbor is much louder than any others, pay attention to two neighbors, even if the weaker one is below the sliding threshold. Paying attention to no more than three neighbors may help prevent frogs from inhibiting their calls too frequently in crowded or noisy environments, says Greenfield.

Because the ancestors of frogs and insects split apart more than 540 million years ago, the profound similarity in their calls and the mechanisms used to generate them are probably not due to shared history. Instead, suggests Greenfield, "in the physical world, only a limited number of options are available to solve the problem of signaling in a noisy environment. In this case, evolution in both frogs and insects may have found the same solution."

That's a plausible notion, agrees Peter M. Narins, a behavioral ecologist and frog communication expert at the University of California, Los Angeles. "It is the living environment that is providing the selection pressure ... [so] similar solutions have emerged"--giving frogs and insects the same song.