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A male European common frog embraces a female in a sometimes two-day mating dance called amplexus. Eventually the female lays a clutch of eggs that is immediately fertilized by the male. However, gangs of males scour the pond for newly laid clutches and fertilize them again. *(Credit: Miguel Vences)*

Clutch piracy revealed as novel mating strategy in European common frog

By Robert Sanders, Media Relations | 15 September 2004

BERKELEY – One of Europe's most common backyard frogs has been keeping a secret that, despite centuries of study and thousands of published papers, has only now been discovered in ponds in the Pyrenees.

The European common frog, Rana temporaria, has long been thought to have a straightforward breeding strategy - one lucky male grabs the female and fertilizes her eggs as soon as she releases them into the water. End of story.

But that's not the end of the story, according to Spanish researcher David R. Vieites, now a postdoctoral fellow at the University of California, Berkeley's Museum of Vertebrate Zoology. In high-altitude ponds in the Pyrenees, on the border between Spain and France, so many males are vying for fatherhood that they pirate the egg clutches after they're laid. Grasping them as they would a female, they release sperm in the floating clutches, often successfully fertilizing the eggs left unfertilized after the initial encounter. In one pond studied, 84 percent of all clutches had been fertilized by more than one male.

In addition, numerous male frogs typically gang around the egg clutch for their turn at fertilization. According to Vieites, genetic analysis of the eggs in a single clutch shows fertilization by as many as four separate males, including the male that actually had embraced the female.

"This is the first example of such a complex mating behavior in amphibians undergoing external fertilization," Vieites said. "Because of a population excess of males, the males found a system to reproduce without the female."
He and colleagues in Spain, Germany and The Netherlands report their findings in the Sept. 16 issue of Nature.

This eager male has clasped the egg clutch even while it is being fertilized by the male clasping the female. This sneaky strategy allowed the interloper to fertilize 95 percent of the eggs in the clutch. *(Credit: David Vieites/UC Berkeley)*

Vieites also noticed a possible female response to this so-called "clutch piracy." Many females delayed release of their eggs until no other males were around, often floating around for several days with a male onboard before releasing eggs. Vieites noticed, too, that some females were releasing their eggs underneath other clutches to hide them from prowling males.

The European common frog, or brown frog, is frequently seen and heard during spring and summer months east of the Ural mountains in Russia, and occurs over a large range of altitude, from sea level to about 2,600 meters (8,500 feet). While studying high altitude populations in an attempt to understand how they adjust to short breeding seasons and survive dry, freezing temperatures, Vieites, then at the Universidade de Vigo in Vigo, Spain, was surprised to see males embracing clutches. He and his colleagues spent two years in the field observing this behavior, and took tissue samples to test the paternity of the eggs in numerous clutches.

What they uncovered was a strategy apparently linked to the unusually skewed operational sex ratio in the Pyrenean ponds, that is, the ratio of eager males to available females. For every female frog there were between four and 10 male frogs in a pond about half the size of an Olympic-size swimming pool. Since male frogs fertilize the female's eggs only after they're laid, there is no opportunity, as with animals that undergo internal fertilization, for more than one male to impregnate a female. And unlike the females of some frog species, the common frog will not lay eggs if clasped by two males.

Since as many as one-third of the eggs may not be fertilized by the first male, however, the opportunity exists for other males to fertilize the remaining eggs in the clutch. The researchers found that without clutch piracy, between 65 and 85 percent of eggs - and sometimes as little as 20 percent - were fertilized. The percentage was about the same with clutch piracy, but averaged 90 percent if, as Vieites observed, one or more of the later frogs forced open the clutch and fertilized the interior eggs.

The common frog is known throughout its range as an explosive breeder once the ice melts in spring, but what may have hampered observation of this unusual behavior is the fact that at lower elevations, breeding typically takes place at night. Because of cold nighttime temperatures in the Pyrenees, however, the frogs breed during the day, allowing Vieites to observe the animals' breeding strategy.

Vieites found that, because of the overabundance of males, each breeding female in a pond typically is surrounded by a half-dozen or more eager males vying to embrace her in a tight, sometimes suffocating grip called amplexus. Even after the female has allowed a male to clasp her, the surrounding males will often jostle the pair in an attempt to dislodge the male.

After as much as two days of amplexus, the female will lay a clutch of eggs, which are immediately fertilized by the male. During this time, however, various males typically follow the pair around the pond and, after the female has laid the eggs and the parents have left, embrace the clutch and fertilize it again. At other times, gangs of males search the pond for newly laid clutches and fertilize them again within an hour or two of being laid. Often, males who fertilize a clutch in the normal way later join a gang to engage in clutch piracy.

To determine the paternity of the fertilized eggs, which can number between 300 and 3,000 in this species, Vieites gathered 16 separate clutches and took tissue samples from the original parents and the pirates. With colleagues at the University of Konstanz, Germany, and the University of Amsterdam, The Netherlands, he analyzed the tissue samples genetically to show that clutch piracy leads to a greater percentage of fertilized eggs in the clutch, as well as clutches with as many as four fathers.

Vieites noted that this unusual mating strategy is a good way for the frog population to ensure that as many genes as possible are passed on to succeeding generations, particularly when there are far more males than females. Despite the lack of reports of similar behavior elsewhere in Europe, clutch piracy may even be common in Rana temporaria, he said. Vieites plans to continue his studies in the Circo de Piedrafita area of the Pyrenees in Spain, in order to understand better the origin of the behavior, and to investigate the importance of the male-female ratio.

"This could be a really good model to help us understand how sexual selection arose in vertebrates, such as amphibians, that developed external fertilization," he said.

Vieites recently joined the AmphiaWeb project, based at UC Berkeley, to sequence four genes from each of the 524 known species of salamanders and the 168 known species of their close relative, the caecilian. The goal is to fully understand the evolutionary tree of amphibians, all the way down to its roots.

Vieites' colleagues in the studies were Sandra Nieto-Roman and Antonio Palanca of the University of Vigo, Marta Barluenga and Axel Meyer of the Lehrstuhl fur Zoologie und Evolutionsbiologie at the University of Konstanz, and Miguel Vences of the Institute for Biodiversity and Ecosystem Dynamics at the University of Amsterdam.

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