## Courtship and Mating Behavior in the Axolotl

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An essential component of the natural history of any species is a description of its mating behavior. Although references have been made to the courtship behavior of axolotls (e.g., Houck, 1977; Armstrong & Duhon, 1989), no complete description is available in the literature. Using time-lapse videography under red light in a dark room, I have observed courtship and mating patterns in axolotls. These behaviors appear to be similar to those that have been described for other *Ambystoma* (e.g., *A. talpoideum*, Shoop, 1960).

The initial stage in courtship consists of each animal nudging the other with its snout, first along the flank and then around the cloaca. This leads to the "waltz" behavior described by Shoop (1960) for *A. talpoideum*, in which each animal presses its snout to the other's cloaca, and the pair moves in a circle. After several minutes of waltzing and circling, the male interrupts the sequence by moving away from the female, who follows closely behind, often touching his tail with her snout. During this stage of courtship, the male slowly shakes his tail from side to side with an undulating motion that begins in the posterior part of his body and resembles the "hula dance" performed by male newts (*Notopthalmus viridescens*; Verrell, 1982). Unlike newts, however, the female also shakes her tail while following, although not as consistently as does the male.

The female follows the male for a brief period, then the male pauses and lowers his cloacal area while vigorously shaking his abdomen and tail. He deposits on the substrate a spermatophore, a small structure consisting of a cone-shaped, jelly-like base with a white, sperm-containing cap. The process of spermatophore deposition lasts perhaps half a minute, and then the male resumes walking forward. Although males will deposit on a smooth surface, spermatophores deposited on these substrates will not adhere well or maintain the upright orientation necessary for the female to pick up the sperm cap. (In the I.U. colony, breeding pairs are provided with smooth stones to which to attach spermatophores.)

After the male deposits a spermatophore, he moves forward one body length, and the female continues to follow him. Once she is positioned with her cloaca over the spermatophore, the male moves off. The female then lowers her cloaca over the spermatophore while rapidly shaking her tail. At this point her behavior is almost indistinguishable from that of a male depositing a spermatophore.

After the female has retrieved the sperm cap, the two animals move independently. Eventually, nudging and waltzing are re-established. This stage of courtship is usually more brief during the second and subsequent encounters, and the female rapidly begins following the male again. The entire process of courtship and sperm transfer is repeated several times during the course of an encounter.

Male axolotls will deposit spermatophores on top of any other spermatophores that they encounter. This behavior has been described for other water-breeding salamanders and may represent an attempt to ensure that the female will be inseminated by the sperm of the male encountering the spermatophore, for the female can pick up only the uppermost sperm cap (Arnold, 1977).

It appears that physical contact provides stimuli that are necessary for the male's deposition of spermatophores. I have done experiments in which a male and female are separated by a plastic mesh fence, and, although I have observed tail-shaking by males,

I have never found spermatophores in the arena under these circumstances. (Animals will, however, breed in these arenas without the intervening fence.) Similarly, the contact that the female maintains with the male while following appears to be crucial for the success of the sperm transfer; although I have occasionally observed females encountering and picking up spermatophores that have been deposited up to several hours before, such instances are rare.

## Literature Cited

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