REPRODUCTION IN THE SMOOTH NEWT, *TRITURUS VULGARIS*

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As anyone who has tried will know, it is very difficult to obtain information on the way in which male mating success is determined in newts and salamanders (Order Caudata), mainly because it is almost impossible to observe the activities of individual animals in the natural environment. Consequently, we are forced to rely on rather indirect data to provide us with the information we need. The approach that I favour is one which combines field- and laboratory-based observations and experiments. Field data on the dynamics of breeding populations can tell us much about how a male's mating success is constrained by factors external to him, such as the availability of sexually responsive females bearing eggs for fertilization. Laboratory studies can reveal details of the behavioural strategies a male can enjoy in order to inseminate such females. And finally, behavioural experiments coupled with more physiological investigations can indicate how a male's mating success is constrained by events occurring within his own body, such as the process of sperm formation. Needless to say, all of these factors must surely interact in complex ways in order to produce the patterns of individual male mating success which occur in natural populations.

Over the last six years, I have been investigating the way in which male mating success is determined in our most common tailed amphibian, the Smooth Newt (*Triturus vulgaris*). This work has adopted the multidisciplinary approach outlined above. Here I can only present a brief summary of the major results of this work. Before I start, I have great pleasure in acknowledging a number of other biologists with whom I have collaborated: Tim Halliday, Dave Sever, Helene Francillon, Norah McCabe and Miriam Griffiths.

Male smooth newts exhibit two behavioural strategies which enable them to inseminate females. The first is for the male actively to court the female; he stimulates her with his courtship display, and then inseminates her by transferring at least one spermatophore. The second strategy is for the male to interfere in an ongoing courtship, and quite literally 'steal' an insemination by behaving in a sneaky way. This second, competitive strategy should be most frequently adopted by males in natural populations at those times in the breeding season when responsive females bearing eggs for fertilization are least frequently encountered. Such a time is when females are busy laying their eggs in the leaves of water plants and are not responsive to male courtship.

In a study of the dynamics of a Smooth Newt breeding population, we found that, in mid-summer, females tend to lay their eggs in a very synchronized manner, *en masse*. This observation led us to predict that competition between males for responsive females should be particularly intense during this period. We are now testing this prediction by observing male sexual behaviour in a natural population; our preliminary results suggest that, during the egg-laying period, many of the sexual encounters we see involve males adopting the sneaky, competitive strategy described above. In this way, they obtain opportunities to inseminate the few responsive females which are available.

However, it does not matter how many responsive females are available to a male if he has insufficient sperm to fertilize their eggs. After all, it is the fathering of offspring, not simply the transfer of sperm, that is the goal of reproduction in male animals. As part of a larger study of the annual reproductive cycle of the Smooth Newt, we investigated the issue of sperm availability by examining the structure of the testes of males collected at different times of the year. The picture which emerges is one which is typical of amphibian species which live in temperate regions. Within any one breeding season, males seem to have a limited amount of sperm in their testes and associated ducts. This is a consequence of the way in which sperm are made; sperm for use within any one breeding season are formed in the previous year. Incidentally, female Smooth Newts yolk their eggs in a similar manner. What is more, this long-term limitation in overall sperm supply appears to be accompanied by a shorter-term limitation in spermatophore availability. This is indicated by the observation that an interval of more than one day is required between two courtship encounters if the male is to deposit the same number of spermatophores during each encounter. We think that this is due to a temporary depletion of the materials necessary to produce spermatophores; these materials are secreted by at least two clusters of glands situated in the male's cloaca.

All of this information can be integrated to provide a general picture of the determination of mating success in male smooth newts. During the breeding season, the availability of both eggs for fertilization and sperm to fertilize them vary over time. At the beginning of the season, responsive females bearing such eggs are relatively abundant and sperm are freely available. However, as the season progresses such females become harder to find and males compete amongst one another for opportunities to inseminate them; at the same time, the males' sperm supply becomes depleted, and their testes make sperm for use in the next, not the current, breeding season.

As is usually the case when one does research, the work that led to the conclusions discussed above has also led us to ask many other questions about the reproductive biology of smooth newts. For example, we know that the size of a male's testes, and thus the number of sperm he can produce, depends on his body size; this depends on his growth rate. One area we are now pursuing concerns the relationships between an individual's size, his age and the amount of effort he invests in reproduction. It is certainly clear that much remains to be done.