## The arms suppliers in predator-prey arms races

The fascinating description by Brodie and Brodie (BioScience 49: 557-568) of the "arms race" between salamanders and garter snakes currently underway on the west coast of the United States is a beautiful illustration of the coevolution of predator and prey. But it neglected to discuss the arms supplier! In some areas, common garter snakes (Thamnophis sirtalis) are somewhat resistant to the toxic principle of the rough-skinned newt (Taricha granulosa). The toxic principle is tetrodotoxin (TTX), which was named for the puffer fish order Tetrodontiformes. It is these puffer fish that are consumed in the Japanese delicacy known as fugu, with sometimes disastrous results (see Prince 1988).

As Brodie and Brodie mention, TTX is found in a broad range of invertebrates. In the last decade it has become clear that the toxin is actually produced by bacteria, including Alteromonas, Vibrio, and Pseudomonas species (see Prince 1988). It is a current paradigm of microbiology that all bacteria are essentially ubiquitous at some level, with the selection pressure of the local environment encouraging the abundance of any particular species at any particular place. The remarkable toxic newt, like the other "users" of TTX, has thus not only evolved at least partially TTX resistant sodium channels, as has its garter snake predator, but also developed some mechanism to encourage the growth of TTX-producing bacteria in or on its skin. Kodama et al. (1986) described exocrine glands

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on the skin of the puffer fish genus *Takifugu* that expel their TTX-rich contents when the fish is attacked, and perhaps these newts possess similar structures. It would be interesting to know if the presence of such structures is correlated with the possession of TTX; such a finding might explain why only some geographic races of the newt possess the toxin. In any case, the role of bacteria in the arms races between eukaryotes should not be ignored; what does the newt have to "pay" for its defense system?

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Prince RC. 1988. Tetrodotoxin. Trends in Biochemical Sciences 13: 76–77.

## Response from Brodie and Brodie:

Roger Prince raises the interesting and critical question of where the toxicity of rough-skinned newts comes from. We did not address this problem in our article because at this point little is known about the production and origins of tetrodotoxin (TTX) in newts. In fact, we are currently trying to determine the source of individual, population, and species variation in levels of TTX in the genus Taricha. To explore these question, we are employing a series of population crosses and common garden experiments, along with high-performance liquid chromatography (HPLC) techniques to quantify TTX levels (in collaboration with Charles Hanifin, a graduate student at Utah State University).

Although bacterial symbionts have

been implicated in TTX production in other taxa, several observations make such a source less clear for Taricha. First, all species of newts that have been tested appear to possess at least low levels of TTX, suggesting some degree of phylogenetic constancy (Brodie et al. 1974). Second, recent investigations of TTX production by bacteria (Vibrio alginolyticus; Matsumura 1995) have suggested that some of the earlier results may be suspect; HPLC peaks identified as TTX may actually be a substance from the bacterial growing medium with similar chromatographic activity. In any event, the possibility that TTX in newts is produced by bacteria is quite real and exciting, and we are grateful to Prince for raising the point. If it turns out that a third party is the supplier of chemical weapons in the newt-snake arms race, then we will be forced to rethink the dynamics of predator-prey coevolution to incorporate behind-the-scenes arms dealers.

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Editor's Note: The feature article by Elizabeth Norton Lasley in this issue also addresses the question of where Taricha gets its toxin.