# Phylogeny and evolution of predator defense in whirligig beetles

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## Abstract

Predation may be seen as a sequence of events: detection, identification, approach, capture and consumption. Arms races between predator and prey have resulted in evolution of a variety of predator-prey systems. This thesis deals experimentally and theoretically with predator defense using whirligig beetles as study organism. Whirligigs live and feed on a variety of freshwater surfaces, often gathering in large aggregations that function mainly in predator defense. From paired pygidal glands the whirligig beetles produce a noxious secretion used in predator defense. The pygidial secretion consises of: a high molecular fraction and a scented volatile fraction. All species produce the high molecular norsesquiterpenes, not all synthesize the volatile fraction (e.g. *Gyrinus minutus* and *G. opacus*) (I). A major theme of this thesis is the role of the volatile secretion in predator defense and signaling (I, II, and III). I show that the volatile secretion functions as an alarm substance in both intra- and inter specific communication. Although only whirligigs producing volatiles are able to use their secretion as an alarm signal, whirligigs lacking volatiles are alerted by volatiles produced by other species (I). Presence of the volatile fraction seems to correlate with group living, habitat choice and predator type (II , III). Lack of volatile secretion seems to make whirligigs more vulnerable to fish predation (II).

Invertebrate predators are often ignored as selective agents in whirligig evolution, however both backswimmers and fish are likely whirligig predators (paper III). In waters containing fish, backswimmers and *G. minutus* are generally concentrated in areas containing emergent vegetation. I show that *G. minutus* (lacking volatiles) survive a backswimmer attack more often than *G. aeratus* (with volatiles) (III). The experimental results suggest that each whirligig species is adapted to defend itself against the predator it is most likely to encounter. Consequently, the pygidial secretion including the volatile fraction is a more effective repellent of fish than of backswimmer. These results suggest that volatile secretions play multiple roles in whirligig anti-predator behavior.

It has also been suggested that whirligig beetles are aposematic using their aggregating behavior as a signal of noxiousness. This is an underlying assumption in this thesis. In the theoretical part, I develop a phylogenetic approach to explain the concept of aposematism stressing its historical nature. Concepts, involving change such as aposematism, are beneficially treated as historical concepts of events. To answer the question *how* aposematism has evolved, we first need to know *where* it has evolved. The *Gyrinus* phylogeny based on absence /presence coding of morphological characters (V) is an important component in explaining whirligig behavior and testing the hypothesis of aposematism.

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