**Are burrowing snakes digging their own evolutionary grave?**

Vivek Philip Cyriac

IISER-TVM Centre for Research and Education in Ecology and Evolution (ICREEE) and School of Biology, Indian Institute of Science Education and Research Thiruvananthapuram, Thiruvananthapuram, India

Why is there variation in the number of species between different groups of animals and plants? Why do some clades seem to be more ‘evolutionarily successful’ with a higher number of species than other? For instance, there are over 10,000 species of birds but just two species of tuataras (lizard-like reptiles from New Zealand) even though both groups originated around the same time. Differences in diversification rates — the overall rate at which new species are accumulated (speciation rate) and removed (extinction rate) — often explain such huge variations in the number of species in different groups. Variations in diversification rates across lineages are generally associated with the evolution of some trait or key innovations that allows some species to diversify rapidly.

Some traits also hinder diversification by increasing extinction rates, and these are termed evolutionary dead-ends. Ecological specializations are often considered as evolutionary dead-ends. Specialization allows species to outcompete generalist but may hinder their ability to adapt to environmental change and thus increase their chances of extinction. However, there appears to be mixed support for this hypothesis. Some studies indicate that specialization decreases diversification while many others suggest that specialization either increase diversification or has no effect. One reason for such confounding results is that species can be specialists on one resource axis while being generalists on another axis. For example, a species could be a dietary specialist feeding on a specific set of prey but could occupy a broad climatic niche. However, if a trait imposes specialization along multiple axes, such traits could potentially limit diversification. Fossoriality, the tendency to burrow and live underground, is one such trait that imposes specialization along multiple axes. Burrowing reptiles, apart from their smaller size, have highly specialized skull morphologies for burrowing into the soil. Constraints on the head shape and size also constrain feeding ability restrict them to soft-bodied prey. Such adaptation to a fossorial lifestyle makes them specialized along multiple axes limiting their ability to adapt to environmental change.

In our recent study, we tested the hypothesis that fossoriality in reptiles increases extinction rates using a comparative phylogenetic approach. We collected information on habitat from several books and published papers for 2078 species of squamate reptiles (lizards and snakes). We categorized species as being fossorial and non-fossorial and mapped these traits onto an already available phylogenetic tree of squamate reconstructed from 52 genes. We then used state dependent speciation and extinction models to estimate speciation and extinction rates between character states, in our case fossorial and non-fossorial taxa. We also estimated transition rates — the rates at which a lineage change states, i.e., from fossoriality to non-fossoriality and vice versa. We compared these models with complex character-independent null models and assessed which models fit our data better. We performed our analyses first on the whole tree and then on the lizards and snakes separately.

Our results indicate that fossorial snakes have considerably lower speciation and higher extinction rates compared to non-fossorial snakes. We also found that transition from fossoriality to non-fossoriality was much lesser compared to vice versa, meaning once a snake lineage becomes fossorial, it experiences higher extinctions with no turning back. Interestingly we did not find the same pattern in lizards. Both fossorial and non-fossorial lizards had similar rates of speciation and extinction while transition rates were higher from fossoriality to non-fossoriality.

But why do we find different patterns in lizards and snakes, after all, snakes are phylogenetically legless lizards. In general, snakes seem to be more specialized than lizards in several aspects. The most obvious is in their overall appearances with snakes having an elongated cylindrical body while body form in lizards is highly varied. Some lizards are dorso-ventrally flattened like many geckos; some are laterally compressed like most Chameleons, while some lizards like the slow worm and worm lizards are elongate, cylindrical and limbless, and look just like snakes. Apart from body form, snakes are chemosensory specialists relying on their ability of smell to sense their environment while lizards use combinations of vision, smell, and hearing. Overall, the degree of specialization varies between snakes and lizards, and fossorial snakes may represent an extreme on this specialization spectrum.

Our study highlights the importance of considering multiple axes and degree of specialization to understand variation in diversification rates. Apart from evolutionary insights, such studies also provide an understanding of how different groups of animals have coped with environmental change. Such understanding is crucial in evaluating how different groups of animals adapt to the current rapid changes in the environment.

**Original Article:**

Cyriac, V.P. and Kodandaramaiah, U., 2018. Digging their own macroevolutionary grave: fossoriality as an evolutionary dead end in snakes. Journal of evolutionary biology. 31: 587-598. doi: 10.1111/jeb.13248