Learning & Behavior (2025) 53:141–142
https://doi.org/10.3758/s13420-024-00649-w

OUTLOOK

Just keep exploring: Genetics of fish niche adaptation

Kathleen M. Munley[1]

Accepted: 13 September 2024 / Published online: 30 September 2024

Summary
Although the diversification of species has fascinated researchers for centuries, we know remarkably little about how behavior influences niche adaptation and the genetic mechanisms through which behavior evolves. In their recent study, Sommer-Trembo et al. (*Science, 384,* 470-475, 2024) demonstrate a critical role for the regulatory gene *cacng5b* in modulating phenotypic variation in exploratory behavior in one of the most exceptional adaptive radiations: the African cichlid fishes of Lake Tanganyika.

Keywords Adaptive radiation · Behavioral type · *cacng5b* · Cichlid · Exploratory behavior · Gene editing

A longstanding central question of evolutionary biology is how new species evolve. Speciation is a key component of adaptive radiation, a phenomenon in which an ancestral species rapidly evolves into new descendent species via their diversification into novel ecological niches. The importance of ecological and morphological traits in promoting adaptive radiation has been investigated extensively, and in recent years, the advent of sophisticated bioinformatics and transcriptomic analyses has enabled researchers to examine the genetic underpinnings of adaptive radiation. By comparing the sequences, structures, and expression of genetic transcripts, studies have revealed that minute changes in these features can have monumental impacts on life-history and physiological traits, which can ultimately promote the evolution of new species.

But what *drives* this variation in genetic material? One possibility that is relatively understudied is behavior. In nature, there is considerable variability in behavior across taxa, and behaviors can differ substantially among closely related species, different populations of the same species, and even within a population. The mechanistic complexity of behavior, from physiological processes to neural circuitry, provides numerous avenues through which natural selection can act to produce differences in behavior. Importantly, many behaviors directly affect reproduction and survival, such as courtship displays, parental care, territorial defense, foraging, and predator avoidance and, thus, are essential to an animal's fitness. Behavior is also critical for macroevolution by facilitating processes such as reproductive isolation, interspecific competition, and speciation. Although researchers have speculated about the significance of behavior in adaptive radiation, its functions in diversification and ecological niche specialization, especially within such a rapid evolutionary timescale, have yet to be experimentally tested.

To address these outstanding questions, Sommer-Trembo et al. (2024) integrated behavioral, genomic, and gene editing approaches to examine how variation in behavior and its underlying genetic mechanisms contribute to niche adaptation in African cichlid fishes. Cichlids (family Cichlidae) are a geographically widespread group of teleost fishes consisting of over 1,700 species divided across African, Neotropical, and Malagasy/Indian clades that show exceptional diversity in their life-history strategies, social structures, and reproductive systems (Maruska et al., 2022). Sommer-Trembo and colleagues specifically focus on the cichlid species inhabiting Lake Tanganyika, a large freshwater lake located in the Great Rift Valley. The oldest of the East African Great Lakes, Lake Tanganyika was formed 9–12 million years ago and is exceptionally speciose, consisting of genera from 22 different teleost families, including perhaps the most phenotypically diverse cichlid assemblage in the world. The cichlid fishes of Lake Tanganyika are comprised of ~240 species that evolved from a common ancestor over 10 million years ago and, thus, constitute one of the largest extant adaptive radiations (Ronco et al., 2021). Additionally, this group has been widely studied in the fields of ecology and evolutionary biology, enabling the authors to map behavioral measures onto ecomorphological and genomic datasets to uncover potential relationships between genotype and behavioral phenotype across species.

In this remarkable series of experiments, Sommer-Trembo et al. quantify a single behavior, exploratory behavior, in over 700 wild-caught individuals from 57 different cichlid species using semi-natural ponds on the shore of Lake Tanganyika. The authors specifically chose to measure exploratory tendency, or a willingness to explore novel environments, because it is easily and readily quantifiable, has established experimental procedures, is heritable

✉ Kathleen M. Munley
kmmunley@ucla.edu

[1] Department of Integrative Biology and Physiology, University of California Los Angeles, 610 Charles E. Young Drive South, Los Angeles, CA 90095, USA

across generations, and shows a high level of individual consistency and repeatability, referred to as a behavioral type or "animal personality" (Munson et al., 2020). Notably, exploratory behavior has been linked with cognitive performance (e.g., learning, problem solving) and fitness in field and laboratory studies of fishes, birds, and rodents, including mate choice, courtship behaviors, habitat and territory selection, and dispersal, suggesting it may be an important driver of macroevolutionary events. Sommer-Trembo and colleagues used a standardized open-field test to show that exploratory tendency (defined as the relative proportion of pond area visited by the focal fish over a 15-min period) is variable across species. The authors also used previously collected environmental and morphological data and statistical modeling to show that more benthic, deep-bodied species have a higher exploratory tendency than more pelagic, slender-bodied species, suggesting that niche specialization involves both morphological and behavioral traits.

To investigate the genetic basis of species variation in exploratory tendency, the authors used published genomic data to determine allele frequencies at single-nucleotide polymorphisms (SNPs), or variants at a single base position in a DNA sequence, and then examined potential relationships between exploratory tendency and genetic variants by combining statistical, phylogenetic, and data simulation methods. Sommer-Trembo and colleagues found that, of the nearly 1,200 highly associated genetic variants, one SNP in particular, which is located in the promoter region of the regulatory gene calcium voltage-gated channel auxiliary subunit 5b (*cacng5b*), is strongly correlated with exploratory tendency. The authors further confirmed this association using available transcriptomic data and showed that *cacng5b* expression in the brain is negatively correlated with exploratory tendency in 43 cichlid species. Sommer-Trembo et al. validated the phenotypic effects of this locus by generating mutant cichlids (*Astatotilapia burtoni*) containing a genetic deletion immediately after this SNP via CRISPR/Cas9 gene editing and quantifying exploratory tendency. They determined that mutants have a higher exploratory tendency than control fish, demonstrating a causal relationship between this SNP and exploratory behavior. While the role of *cacng5b* in controlling behavior is unknown, this gene encodes a protein that regulates AMPA glutamate receptor density and distribution and, thus, has been implicated in synaptic plasticity and MAP kinase signaling in other vertebrates (Milstein et al., 2007). Additional research is needed to further explore the functions of *cacng5b* and to identify other candidate genes that modulate exploratory tendency, as *cacng5b* is likely part of a larger network of genes that regulate this behavior.

Collectively, the results of this impressive study provide promising evidence that behavior promotes speciation and evolutionary diversification. It is important to note, however, that exploratory behavior is one aspect of an animal's complex, diverse behavioral repertoire. Moreover, while exploratory behavior is associated with reproduction and survival, it is not the most direct behavioral correlate of fitness. The authors' rationale for studying exploratory behavior is warranted, especially given the relative simplicity of its behavioral paradigms and the expansive nature of their experiments. Yet, this choice overlooks what I, as a behavioral neuroendocrinologist, view to be a major strength of the African cichlids: their remarkable diversity in reproductive strategies and social systems across species and their dynamic variation in social behaviors, such as courtship, reproductive tactics, parental care, and social learning and cognition. In this regard, the authors miss an opportunity to harness this rich aspect of these species to provide unprecedented insight into how these behaviors that are so critical for fitness have evolved. While further studies are necessary to identify additional behavioral traits and genes that contribute to macroevolution, Sommer-Trembo et al. shed light on the importance of behavior in contributing to niche adaptation. Furthermore, their work suggests that the diversification of a behavioral phenotype, a willingness to explore novel environments, greatly impacted the evolutionary trajectory of one of the largest and most fascinating adaptive radiations on Earth: the African cichlids of Lake Tanganyika.

Funding The author is supported by National Institute of General Medical Sciences NRSA Postdoctoral Fellowship F32GM153130-01.

Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflicts of interest The author has no conflicts of interest to disclose, financial or otherwise.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Maruska, K. P., Anselmo, C. M., King, T., Mobley, R. B., Ray, E. J., & Wayne, R. (2022). Endocrine and neuroendocrine regulation of social status in cichlid fishes. *Hormones and Behavior, 139*, 105110. https://doi.org/10.1016/j.yhbeh.2022.105110

Milstein, A. D., Zhou, W., Karimzadegan, S., Bredt, D. S., & Nicoll, R. A. (2007). TARP Subtypes differentially and dose-dependently control synaptic AMPA receptor gating. *Neuron, 55*(6), P905–P918. https://doi.org/10.1016/j.neuron.2007.08.022

Munson, A. A., Jones, C., Schraft, H., & Sih, A. (2020). You're just my type: Mate choice and behavioral types. *Trends in Ecology & Evolution, 35*(9), 823–833. https://doi.org/10.1016/j.tree.2020.04.010

Ronco, F., Matschiner, M., Böhne, A., Boila, A., Büscher, H. H., El Taher, A., Indermaur, A., Malinsky, M., Ricci, V., Kahmen, A., Jentoft, S., & Salzburger, W. (2021). Drivers and dynamics of a massive adaptive radiation in cichlid fishes. *Nature, 589*(7840), 76–81. https://doi.org/10.1038/s41586-020-2930-4

Sommer-Trembo, C., Emília Santos, M., Clark, B., Werner, M., Fages, A., Matschiner, M., Hornung, S., Ronco, F., Oliver, C., Garcia, C., Tschopp, P., Malinsky, M., & Salzburger, W. (2024). The genetics of niche-specific behavioral tendencies in an adaptive radiation of cichlid fishes. *Science, 384*(6694), 470–475. https://doi.org/10.1126/science.adj9228