The Blue Threadfin *(Ophthalmotilapia ventralis)* is found exclusively in Lake Tanganyika, where it lives along the shore. The female first lays her eggs in a pit in the sand prepared by the male and then takes them into her mouth to incubate. When the female snaps at the egg-like spots on the male's extended ventral fins, the male releases his sperm and the eggs are fertilized. The female keeps them in her mouth until the young hatch – protecting them from predators.

PHOTO: ALEX JORDAN / MPI OF ANIMAL BEHAVIOR

ECHOES OF EVOLUTION: THE CICHLIDS OF LAKE TANGANYIKA

TEXT: CARLA AVOLIO

Lake Tanganyika in East Africa, formed ten million years ago, boasts an extraordinary diversity of species. For decades, researchers have flocked to its shores to study its unique ecosystem. Among them is Alex Jordan from the Max Planck Institute of Animal Behavior in Konstanz, who considers the lake a paradise. With the aid of modern technology, Jordan aims to analyze the behavior of the cichlids that live in Lake Tanganyika.

The Great African Lakes – Lake Tanganyika, Lake Malawi, and Lake Victoria – are some of the oldest lakes on Earth in geological terms. Over millions of years, evolution has taken advantage of this extensive time frame to create a remarkable variety of species. One family of small fish – the cichlid family – is particularly diverse. Today, Lake Tanganyika is home to over 250 species of cichlid, each occupying its own unique ecological niche.

For more than a century, scientists have been venturing to Lake Tanganyika in search of insight into the grand process of evolution. That's because Tanganyika, more than almost any lake on Earth, has been bequeathed the gift of time. A long blue jewel in the chain of African Great Lakes, Tanganyika formed when fresh water flooded the East African Rift as it began tearing the land apart, creating a lake that still stands 10 million years later.

Geologically, that time might be modest, but what evolution has done with it has been nothing short of explosive. With ample time and space, the most recent common ancestor of a cichlid fish gave rise to over 250 new species, each adapted to fit a different niche in the environment. Lake Tanganyika, along with its sister Lakes Victoria and Malawi, became known as Darwin's dream ponds – textbook examples of speciation through evolution, and a destination for those yearning to understand its story.

For those scientists, the goal has always been to unravel the complex paths evolution has taken to produce the spectacular diversity of cichlids we see today. Spending months or years in the wilds, they collected illustrations, descriptions of color and pattern, or skeletons carefully packed for later examination. Today, evolutionary behavioral ecologist Alex Jordan continues this tradition, but he is not collecting bones. He is collecting behavior.

"Lake Tanganyikan cichlids are the most behaviorally diverse of all cichlids, perhaps all fish," says the independent group leader at the Max Planck Institute of Animal Behavior in Konstanz. Species span the range from solitary hunters all the way up to permanent family groups with siblings and cousins helping to care for young. Each species also has its own behavioral variation on themes of aggression, courtship, submission, and cooperation. The ocellated shell-dweller appears to roar when confronted with a rival, while the featherfin cichlid flashes beautiful colors in a dance to deter territorial encroachers.

PHOTO: PAUL NÜHRENBERG

Alex Jordan (front) and his team prefer to study the cichlids of Lake Tanganyika in their natural habitat. Only then can he see the full diversity of their behavior, because interactions with conspecifics and other fish species, as well as various environmental factors, have a significant impact on a fish's behavior.

For Jordan, the dazzling array of behaviors that each cichlid species displays tell an evolutionary tale just as alluring as the famous speciation that the group has undergone. But so far, what we know about the evolution of behavior lags far behind what we know about their morphology. Bringing clarity to this picture is the aim of the Jordan Lab. "Our ultimate goal is to create quantitative behavioral maps for each cichlid species, allowing us to compare entire behavioral phenomes to understand how evolution has shaped the diversity we see today."

Wilderness expedition

So twice a year, Jordan's team make the four-day journey from Konstanz to the Zambian shore of Lake Tanganyika. In the waters, they hope to sow the seeds of a new evolutionary tree – one that connects the lush branches of behavioral diversity.

This goal might seem grand, but getting there is conceptually simple. First, you have to measure the breadth of behavior an animal displays, a once impossible task that has become achievable with modern approaches to tracking and analysis of animal movement. "From a practical perspective, it's quite challenging to bring all this technology to remote locations and record animals underwater," says Jordan, "but having done that, measuring behavior isn't the hardest part."

The hard part is in the second step, which is to answer a deceptively simple question: What exactly is a behavior? Correctly interpreting the function of a behavior represents a real problem here. Take as an example the behaviors that Jordan studies. Some, such as the building of a nest to raise young, the careful tending of a courtship bower, or different methods of feeding, have clear and interpretable functions that few would disagree over. But others are far more difficult to interpret. It is these difficult cases that fascinate Jordan, for whom the most problematic behaviors are also the most interesting. "Social behaviors are some of the most complex and exciting forms," he says, "but they are by definition an interaction between animals, and an interaction that we're not part of." To map these behaviors on to an evolutionary tree and make reasonable comparisons among them, we have to know both what they are, and also what they are for. Jordan likens the problem to that faced by early taxonomists when receiving a jumble of bones in boxes sent from afar: "Without a clear picture of when, where, and why this behavior occurred, we may end up unknowingly building a Brontosaurus out of the bones of a T-Rex."

Long before he became a Max Planck group leader, Jordan was aware of this problem. "My PhD advisor would caution that behavior is a slippery thing," he remembers. And since then, Jordan has been struggling to get a firm hold. In 2019, he and colleagues from Osaka City University made quite a splash when they demonstrated that a species of fish was able to pass the "mirror test" – a behavioral assessment introduced in 1970 and widely regarded as the best indication of self-awareness in non-human animals. Up to that point, only some mammals and crows had passed the mirror test. "This was a great result because it really got people talking about consciousness in animals other than humans," says Jordan. But an uncomfortable truth gnawed at the scientist: "For me, it served most to highlight the gap in our understanding of behavior in species not our own." For Jordan, the fact that a fish passed the mirror test, without any other evidence of self-consciousness, emphasized that apparently equivalent behaviors may have vastly different causes and functions. "A fish and a chimpanzee might both pass the mirror test, but that does not mean they passed for the same reason."

SUMMARY:

In Lake Tanganyika, evolution has produced numerous different species of cichlids, which differ not only in appearance, but also in their behavior.

Researchers are studying the behavior of the fish in their natural habitat so that they can gain a better understanding of the significance of the ecological and social environments of the animals.

By using artificial intelligence, researchers aim to create an atlas of the different cichlid behaviors free from their own preconceptions. This approach will help them investigate how these behaviors have evolved over time.

A 2020 study reinforced this opinion. Interested in whether dominance played a role in social influence, doctoral researcher Mariana Rodriguez taught fish to predict the location of a food reward using light cues. She then placed these informed animals into new social groups and found that while dominant male fish learned to solve the task and were able to act as demonstrators, they were not nearly as effective in this role as subordinate males. Yet computational behavioral analyses by another student, Paul Nührenberg, illuminated an astonishing truth: dominant and subordinate males demonstrated the solution in exactly the same way – so what was the difference? "When the dominant male burst toward a food reward, all the other fish darted out of the way, apparently perceiving this as a threatening behavior," says Jordan. "Yet when the subordinate male performed the same behavior, the response was the opposite. Group members remained close to him and more quickly learned the solution themselves." For Jordan, this was further evidence that the same form of behavior can perform different, even opposite, functions depending on where, when, and how it is expressed, "and this makes evolutionary comparisons of behavior extremely challenging."

This becomes even more difficult the further away from humans we travel on the evolutionary tree, where the form and function of signals become increasingly alien to us. "As humans, we may have an intuitive sense of what a primate or other mammal 'means' or 'intends' when it performs a behavior, but for other animals this intuition fails us," says Jordan. The flick of a fish's fin, or a rapid change in the color of its eye, are signals that mean something for the receiver, but as humans we have little insight into what they may mean. If the goal is to compare behavior across species and evolutionary time, understanding these signals becomes critical. What is the same, what is different, and how can we as external observers make this distinction?

Distant relationship

Yet rather than being a barrier, Jordan believes the taxonomic distance might actually be the key to the problem, allowing us to take an objective perspective on behavior. "Perhaps it is the very thing we find most difficult that gives us the greatest opportunity to understand behaviors that we ourselves do not possess. To achieve this, though, we need help, some way of seeing what we don't see, and interpreting what we can't understand."

This is where the ancient lake meets the modern era. Jordan's team has developed techniques to track the movement and posture of wild fish in some of the most complex visual scenes imaginable, where fish have evolved over millions of years to blend in and camouflage with their surroundings. Aided by machine-learning approaches, the team can then track and analyze the postures, movements, and interactions of fish in their natural habitats, generating a complete description of all the behaviors an individual performs. "While this can be a very powerful step in understanding

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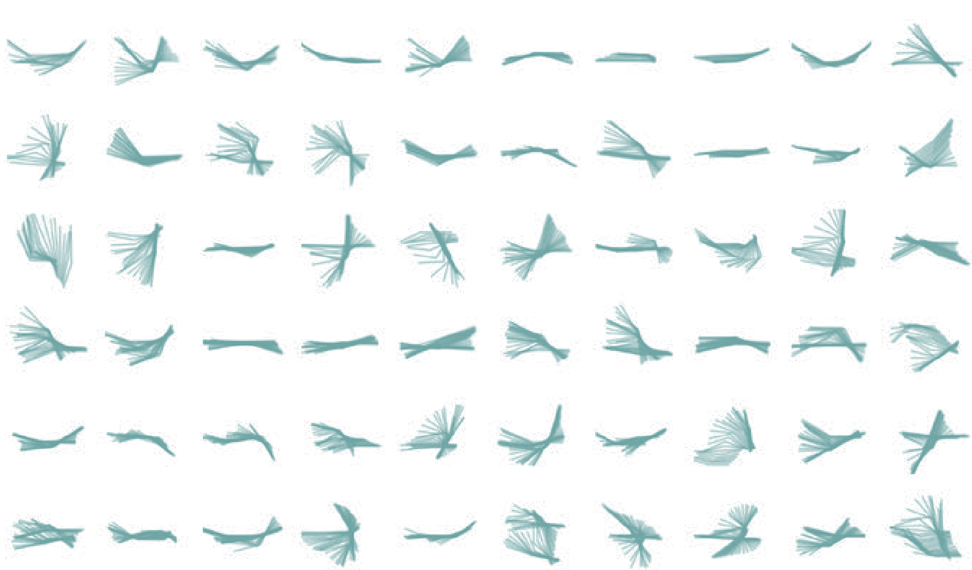

GRAPHIC: PAUL NÜHRENBERG

The individual images show the postures associated with a behavioral element that the researchers previously filmed in the lake. The aim is to digitize all the behaviors of different species and analyze the relationships between the individuals involved.

how evolution has shaped the form and expression of behavior, it is only the first step, it is still the cataloging stage," says Jordan.

Jordan explains that to understand behavior we must do more than simply describe it; we must situate it in the contexts and environments in which it is naturally expressed. He believes this method of perspective-taking can drive us forward: "The goal should not be to translate the behavior of fish, or any other animal for that matter, in human terms, but to contextualize the behavior of animals in terms of their own experience and perception," he says. "We approach this problem from many directions," says Jordan.

Real and digital fish

But to truly understand the function of behavior from the perspective of an animal requires some entirely novel approaches, and in response to this challenge, Jordan and his team are taking their science into uncharted waters. On the most recent expedition to Tanganyika, lab member Jakob Gübel carried with him a strange rectangular box with a curved glass front, capable of withstanding the immense pressures of the lake depths. Inside, safe and dry, was a tablet.

Swimming on the screen is a 3D simulation of a cichlid, which to many human observers is indistinguishable from the real thing. "But a human is not the intended audience," Jordan reminds us with a smile. "This little fish is how we change the cichlids from being study subjects to scientific collaborators." As he plays back an animation of the fish dancing and quivering its tail, Jordan explains that, depending on who is watching, this behavior could be a threat, an invitation to mate, or just a response to being stung by a jellyfish. "And the fish themselves will tell us which it is."

In this way, the behavioral maps Jordan creates for each species can be explored and analyzed to determine their function. Some areas may be novel, species-specific behaviors that do not occur anywhere else; some may be shared and understood by all species; others still may be what Jordan calls "redundant" – different forms fulfilling the same function. With this approach, they take humans out of the loop. "It is the fish who tell us the function of the behaviors," he says, "allowing us to understand how behavior has changed across species boundaries." After a decade of grappling with the slipperiest of problems, the scientist's grip may be beginning to hold.

Jordan does not claim that technological solutions will be a silver bullet in understanding animal behavior, nor that these approaches can "translate" animal behavior into human language. Rather, he says he uses these approaches to ask new questions that can reveal fundamental insights into the evolution of behavior: "And if the only ones with the answers are in a lake thousands of kilometers away, then we will be on the next boat." With more fish species on Earth than all other vertebrates combined, it seems Jordan and his team will be heading underwater for the foreseeable future, to meet their underwater collaborators where they are. ←

CLEANER WRASSE IN THE MIRROR TEST

In the test, researchers applied a colored spot under the jaw of a cleaner wrasse *(Labroides dimidiatus)*, in a location where the fish could not see it. They then placed a mirror in the fish's tank. Once the fish realized it was not seeing a rival, it began to exhibit unusual behaviors: swimming upside-down, flipping around its axis, and rubbing its jaw against the sand as if trying to remove the spot. These actions indicated that the fish understood the mirror was reflecting its own image.

PHOTO: JAKOB GÜBEL

Brave fish: Lake Tanganyika is also home to *Telmatochromis vittatus*. This eight-centimeter-long cichlid lives near the shore and uses crevices in rocks and rubble as hiding places. During the breeding season, the male defends the territory.