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Odd Man Out

Do fish have personalities?

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It's like Hollywood in the fish room of the animal biology department at the University of Illinois, Urbana-Champaign. Dave Ernst, the lab tech, points the camera through a peep hole in a black plastic drape towards a small fish tank, while behind him, postdoc Katie McGhee dips a net into a larger tank of juvenile three-spined sticklebacks, ready to pick out the day's first star. "C'mon, who wants to be famous?" she clucks, transferring a fish via a plastic beaker to the smaller tank to be filmed. The camera rolls.

The selected stickleback does what sticklebacks do—it swims. It circles up and down the smaller tank, pokes around the fake plants at the bottom, then moves back up the water column, its little fish mouth swishing back and forth. Meanwhile, McGhee gets into what she calls "pike position." Crouching behind the tank, she dangles a green ceramic replica of a pike—a common stickleback predator—above the water. At the 3-minute mark, she drops the fake pike into the water and slides it back and forth along the tank's back wall. Upon seeing the intruder, the stickleback freezes in the bottom right corner of the tank. But after a few minutes the fish gets positively cheeky, swimming right up to the pike's head, before seemingly losing interest and meandering off nearby.

After 9 minutes, the stickleback's time in the spotlight is over. There are still about 130 more fish to film before going through the footage to assess individual differences in factors like how

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actively each fish foraged in the tank before the pike appeared and how it responded to the predator's presence. Scientists are finding that fish raised by a father (the species' sole caretaker) tend to take fewer risks with predators than fish raised in incubators. Ultimately, the scientists also hope to probe the genomic underpinnings of this behavioral variation. Or, as they're calling it, the differences in stickleback personality.

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Debate: Do fish have personalities?

Classic "personality" traits include boldness, shyness, aggression, curiosity, sociability, and level of activity.

Though it sounds like an almost heretical term to use for fish, "personality," say McGhee and her boss, Alison Bell, is nothing more than consistent, individual differences in behavior. And in any species—even surprising ones such as squid, birds, and insects—one can find such variability in spades. Meaning that, even if their environment is the same, one individual will consistently act differently from another. Classic traits include shyness or boldness in response to threats such as the presence of a predator, and aggression to conspecifics, but there's also how actively an individual explores a new environment—curiosity, one might say—or how sociable it is, or its general level of activity. While these are the traits most widely studied so far, Bell and others say they're probably just a start. In some cases, personality traits might be heritable, while in others they might develop as a learned response to differences in conditions of an organism's life—the kind of parental care it receives, for example, as in McGhee's experiment, or an influx of predators into its habitat.

Listen to Alison Bell, who studies personality in sticklebacks at the University of Illinois at Urbana-Champaign, and Luc-Alain Giraldeau, a self-described "old school ecologist" from the University of Quebec in Montreal, who doesn't quite buy the idea of animal personality, debate this growing area of research.

Despite the environmental component, personality can be more than just a learned response to environment, since a learned behavior can be forgotten relatively quickly. Bell likens personality to factors such as height or weight, which clearly can have both a genetic and an environmental component, while being more stable. "I would say the key thing to personality is that there is individual variation and individual consistency," she says. That variation and consistency might also explain why some individuals might learn from their environment faster than others.

The field of animal personality has become a fad, with few novel ideas to offer behavioral and evolutionary biology at

It's not at all obvious from an evolutionary standpoint why these consistent individual differences should appear in many species—why one stickleback might repeatedly venture out in search of its next meal while a pike lurks nearby, for instance, but another consistently hides behind a rock until the danger passes.

large, says Luc-Alain Giraldeau.

"People say there's no way a fish can be smart enough" to have what humans call personality, says Bell. "But having personality is actually a stupid thing to do." Consider a species of spider in which particularly aggressive females have a leg up on both fighting off predators and competing for food. That aggression, though, spills over into another context—those females may not be able to hold back from cannibalizing a potential mate, cutting off their chance to reproduce. This is clearly not optimum behavior.[1] The central question for animal personality researchers, then, is how such a range of differences might have evolved. And if these differences are maintained in a population, they must carry some adaptive value. If so, what is it?

Of course, there are many other reasons besides personality for why individual animals behave differently in the same environment. Ants become workers versus drones and bees or naked mole rats take on their roles within the colony due to their genetics or based on strictly environmental cues, like how much nutrition an organism got in development. Alternatively, an organism might come by its role over time, as in bees, who start out as workers and become foragers later in life. A couple key caveats illustrate how personality is different. First, while selection pressures on personality traits would be acting on individuals, in social organisms they'd more often be acting on the group as a whole, since only some individuals are able to reproduce. Additionally, while colony roles tend to be distinct, personality traits are on a continuous gradient; in other words, you can be more or less shy or bold, but you're categorically either a worker or a drone.

Even scientists in the field's inner circle can be skittish about applying the term "personality" to the likes of fish and spiders.

The field is not without naysayers. Even scientists in its inner circle can be skittish about applying the term "personality" to the likes of fish and spiders. Others say the data don't necessarily support the concept that these consistent, individual differences in behavior reflect a distinct phenomenon, whether it's called "personality" or not. The field has become a fad, claims Luc-Alain Giraldeau, a behavioral ecologist at the University of Quebec at Montréal, with few novel ideas to offer behavioral and evolutionary biology at large. "Animal personality does not have the foundations of theory," he says. "So when we find it, we don't know exactly what we've learned about biology."

It's no surprise that animals of all kinds react differently to their surroundings, but for the most part, researchers have historically assumed that an individual organism's behavior follows the rules of maximum fitness in any given situation, changing its behavior as the situation dictates. If the amount of food available in a habitat suddenly drops, for example, or changes location, an animal ups its foraging activity or changes its search

strategy. Variation around this ideal response, in classical models of behavior, was considered to be simply noise.

So when is it personality, and when just "noise" around an optimal response?

But variability among individual animals that persists regardless of circumstances—whether that variability benefits survival or not—suggests there may be more to the story. One of the earliest observations by behavioral ecologists of this type of variability was published by Felicity Huntingford, a functional ecologist at the University of Glasgow, in 1976.[2] Sticklebacks who were bold, she observed—that is, who didn't shy away from predators—also tended to pick fights with members of their own species. Furthermore, individuals measured at different points in their lives tended to maintain the same level of aggression and boldness relative to other members of their group. That consistency in individuals implied that some fish behaved more boldly and aggressively than others not because their circumstances dictated those responses, but because that's just how they were.

In some cases, personality traits might be heritable.

Huntingford's 1976 study lay dormant and rarely cited in the literature, perhaps at best an observational curiosity, for almost 20 years. But in the early to mid-1990s, researchers began to study the continuum of traits such as boldness and shyness in species in which you wouldn't necessarily expect to see them, perhaps most notably David Sloan Wilson, who studied fish at the University of Binghamton in New York.[3] Meanwhile, other labs began observing individual differences in foraging, risk-taking, and other types of behaviors in the wild. Piet Drent's group at the Netherlands Institute of Ecology found that great tits who were quick to explore novel environments—so-called fast explorers—were not very good at picking up on changes to those environments, such as when the researchers moved the food. Birds who were slower to explore, however, were better at switching up the routine. By following a natural population over 5 years, the group provided evidence that these so-called personality traits were heritable.[4] The researchers found that different personality types also seemed to be differentially affected by selection pressures depending on the circumstances. In a year when extra food wasn't present, fast explorers fared poorer than slow, perhaps because they were slow to pick up on this change to their environment.

A more recent example from the avian world also highlights how individual behavioral differences can sometimes be adaptive. As a postdoc at Harvard,

Renée Duckworth wanted to study how a factor such as choice of habitat changes the make-up of the population of two sister species of bluebirds in the northwest United States. “I never intended to work on animal personality,” recalls Duckworth, an evolutionary biologist now at the University of Arizona. “I actually started from the viewpoint of assuming I was going to find a lot of phenotypic plasticity.” The two species she studied don’t coexist, and when western bluebirds colonize areas already inhabited by mountain bluebirds, they force the latter to find new homes. In tracking the animals over several breeding seasons, she found that certain western birds, specifically the aggressive ones, go off to colonize new regions. Those animals also aren’t as attentive parents, so they have fewer offspring. After the colonizers have lived there a while, the more consistently mellow western bluebirds, who also tend to have more offspring overall, come in to take advantage of the newly captured land. The link between aggression, dispersal, and parental behavior is “a whole suite of traits that’s basically integrated into [the animals’] life history strategy,” Duckworth says.

Meanwhile, Denis Réale, a behavioral ecologist at the University of Quebec at Montréal, was also encountering individual behavioral differences that reflected animals’ life histories. While conducting a population genetics study on a group of bighorn sheep on a mountaintop in Alberta, the students tagging the animals once per year told Réale they could predict from how the sheep had behaved last year whether they’d be easy to tag or not. “At first I thought it was kind of funny—an anecdote,” he says. “The more I thought about it, the more I wondered, why do we have this variation in what we would call docility?” They started to track how easily the animals could be handled. The team found that male animals who were more aggressive also reproduced early in life, and those who were more docile sired later. Those aggressive early in life often sired lambs even at 2 or 3 years of age, but rarely survive past 8 years. Docile animals generally didn’t start reproducing until they were 5 or 6, but lived much longer, and ultimately became dominant in the group. Globally, though, they attained the same level of fitness, in terms of number of offspring.[5] Studies such as Duckworth’s, Drent’s, Réale’s and Huntingford’s showed “that there was a relationship between [traits that] was kind of surprising,” says Judy Stamps, a behavioral ecologist at the University of California, Davis. “Basically, it says that for whatever reason, these things are tied together.”

So when is it personality, and when just “noise” around an optimal response? “My pet idea,” says Bell, “is that sticklebacks will behave consistently under high predation pressure but not low [predation pressure],” she says. In a recent study, she took a population of the fish in which aggression and boldness were not correlated and exposed them for a day to hungry rainbow trout predators who were allowed to eat half the prey population. Voilá—in the remaining sticklebacks, the pair of personality traits became linked, with some fish consistently bolder than others, and the bolder ones also consistently more aggressive.

Animal personality researchers say they've observed meaningful and

The association between such traits seems to be heritable, according to Niels Dingemanse, an evolutionary ecologist at the Max Planck Institute for Ornithology in Seewiesen. Offspring of a population of sticklebacks that had a history of predation showed more consistent personalities than offspring whose parents were naïve to predator threats. The study needs to be replicated before firm conclusions can be drawn, says Dingemanse, who did his PhD in Drent's great tit lab, but he suggests that the effect might be due to genetic variation in some complex of genes, which are expressed differently when the population experiences predators. Alternatively, he says that the traits might be regulated by a single gene with a pleiotropic effect—that is, acting on a handful of phenotypes at once. "If there's no predator, that gene is silenced somehow," he speculates, but when the population is threatened it switches on, and "all these things become correlated."[6]

consistent individual differences in organisms including hermit crabs, squirrels, sheep, spiders, and lizards, to name a few.

Animal personality researchers say they've observed meaningful and consistent individual differences in organisms including hermit crabs, squirrels, sheep, spiders, and, lizards,[7] to name a few, not to mention organisms like primates. But calling those differences "personality" remains controversial.

At a behavior meeting in Oxford last December, Bell recalls, one postdoc gave a talk on individual differences in the behavior of aphids, plant-eating insects, in response to their ladybug predators. In the presence of a ladybug, an aphid will either drop from its leaf or hang on; the speaker suggested that some individuals consistently take one route, while some the other, referring to this variance as a personality trait throughout her talk. When it came time for questions, "she got ripped," says Bell, by audience members who claimed the word "personality" shouldn't be used in an insect for such a mundane behavior. But Bell can't see what the fuss is about; if you define personality as consistent individual differences in behavior, that's a definition that applies to more than just complex species. "If that's the definition we want to use, then why do we want to restrict ourselves to one kind of organism?"

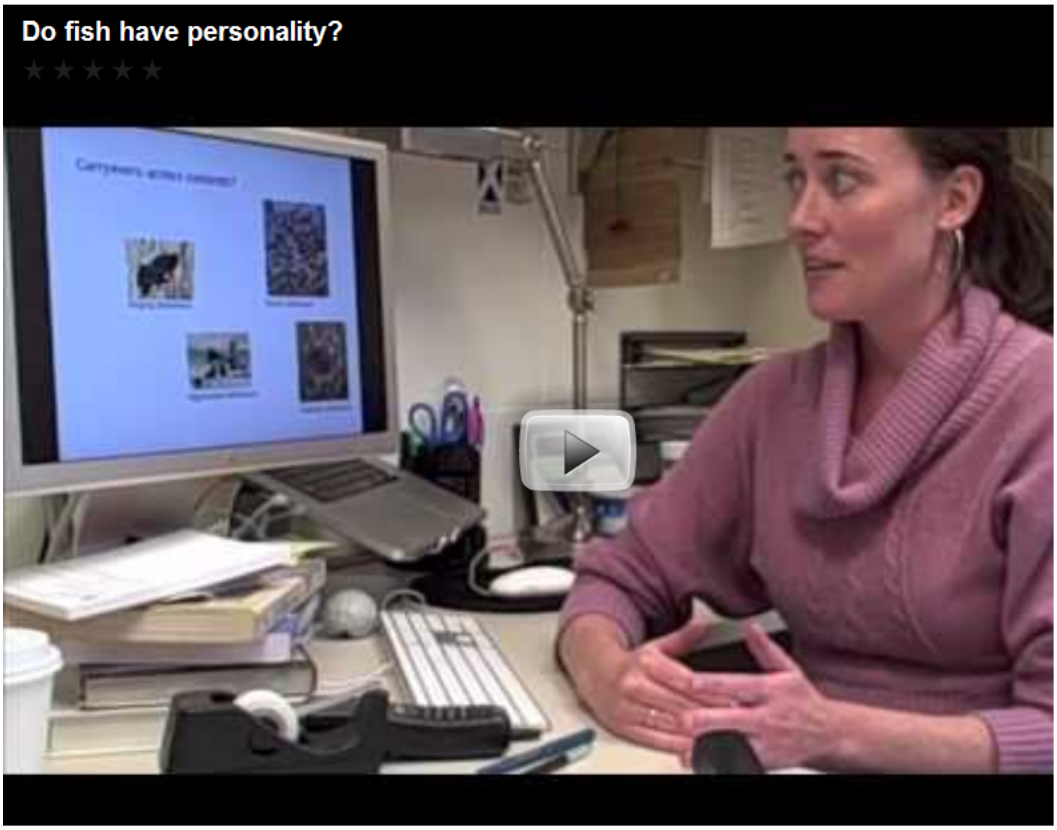
However, some researchers who study such individual differences in behavior eschew the word "personality," instead favoring monikers such as "behavioral syndromes" or "temperament," or simply "variability," in part to sidestep any semblance of anthropomorphizing. "I don't really use the term," says Duckworth. "I think it invokes too much about humans."

Alison Bell can't see what the fuss is about; if you define personality as consistent individual differences in behavior, "then why do we

Terminology, though, isn't the only objection. Evolutionary biologists have studied variation and how it persists for decades, and the same explanations for the persistence of variation in traits like morphology and color should also apply to behavior, says Alex Kacelnik, a behavioral ecologist at Oxford University. The focus on behavioral variation is producing some

want to restrict ourselves to one kind of organism?"

interesting findings, he notes, but he's not convinced that the novel explanations some personality researchers invoke are warranted. Researchers often claim that certain correlated traits reflect personality, but those correlated traits might have a common cause that doesn't have to do with personality, he says. For example, an animal might be willing to forage farther from its home and eat more diverse food for a reason related to personality—because it is generally more receptive to new environments—or simply because it is more mobile, and by nature of that fact, encounters a more varied diet.



What's more, says Giraldeau, animal personality researchers haven't come up with a good theoretical framework that explains why the consistent differences they describe have evolved or predicts which behaviors can be called personality and which are, in fact, merely noise or some other phenomenon. One species might be aggressive in several contexts, from mating to responding to predators, he says, and so might another, but it might not be for the same reason. "I'm not convinced there is a unique phenomenon being addressed here," he says.

Of course, says Dingemanse, studying variation and its adaptive value is nothing new for evolutionary biologists and ecologists. But for the most part, he notes, researchers have looked at traits as averages from within the population or species—that is, some species might be said to be on the whole bolder than others. Previously, scientists have also assumed that traits are fully flexible, meaning that any individual can be as shy or as bold as the situation demands. By focusing on

variation between individuals, not between species or populations, the animal personality field "asks questions that have not been asked," he says. "The study of animal personalities is just the logical continuation of looking at variation in more detail."

If these individual differences are maintained in a population, they must carry some adaptive value. If so, what is it?

Also, existing models in evolutionary theory aren't very good at dealing with correlated clusters of traits, notes Max Wolf, a postdoc at the Centre for Adaptive Behavior and Cognition at the Max Planck Institute for Human Development in Berlin. Aggressive individuals might be bolder and have different styles of exploration than nonaggressive ones, or they might parent differently; what interests personality researchers is how one behavioral trait develops over time and how different behavioral traits interact with each other. Previous scientists "traditionally took a much more simplified approach [of] one trait at a time," he says.

On top of that, says Bell, studies of animal personality have exposed problems with long-held evolutionary models. Take, for example, mate selection, which is based on the assumption that females of a single population all have the same preferences and that they are all equally choosy. But her lab recently published a meta-analysis of studies on a wide variety of organisms that found the opposite.[8] Different females don't all pick the largest, fittest male; just as with humans, there often seems to be no rhyme or reason for mate choice. Yet the fact that classical models are static in this way leads to an inaccurate picture of selection pressures, Bell says.

Animal personality researchers agree that for the field to move forward, it must develop theoretical models explaining how or why stable individual differences might have evolved.[9] One of the first computational models, published by Wolf, Franjo Weissing, and their colleagues at the University of Groningen in the Netherlands posits that individuals differ in their risk-taking behavior, with those that have more to lose, evolutionarily speaking, developing personality traits that could be described as more cautious. Another proposed by Stamps, but with as yet no math to back it up, links suites of personality traits to individual differences in physiology; individuals with a fast metabolism need to consume more resources, thus tend to be bolder and more aggressive.

But so far, no single theory explains the range of empirical data on personality that researchers have amassed. Researchers working on these theoretical models therefore are beginning to test their predictions in the field and the lab. Those tests, says Weissing, will determine whether the concept of animal personality has

much to add to behavioral biology. "In 10 years we will know much more."

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