Do Animals Have Personality?

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The importance of individual differences.

In the scenic Rocky Mountain town of Banff, Alberta, the site of Canada's oldest national park, it is not uncommon to see elk grazing on lawns or near riverside trails. Why are elk wandering about town? The town may act as a refuge from wolves—a species that usually goes out of its way to avoid human contact. But elk "townies," as the locals refer to them, are a new phenomenon. Prior to the 1990s, archaeological and historical records suggest that elk were rarely seen in the town center.

How did the elk become less wary of humans? It turns out that not all elk are brave. Research by University of Alberta doctoral student Rob Found suggests that may take a few bold individuals to lead the way. Found's study is the first extensive research on personality types in any wild ungulate species, but elk are just one of many animals in which personality is being explored. Personality has been identified in organisms as diverse as sea anemones, limpets, fish, birds, rodents, ungulates, spiders, water striders, and lizards, and with new species frequently added to the list, emerging research suggests that personality may exist across the entire animal kingdom.

Animal personality refers to consistency in the types of behavior that individuals exhibit. Behavioral biologists, psychologists, endocrinologists, and evolutionary and developmental biologists are now studying animal personality. Understanding personality in the context of epidemiology may help to inform captive breeding, reintroductions, and the conservation of endangered species, as well as potentially shedding light on disease transmission in humans.

In the case of elk, Found observes both captive and wild elk marked for individual identification and performs personality tests to rank the relative boldness or shyness of each animal. One simple test looks at flight response—the readiness of individual elk to flee on the approach of a human observer.

Found also developed an unusual experimental setup, using wildlife cameras trained on novel objects—things that elk would not typically come across in their natural habitat—to determine their relative boldness. These objects include old bike frames, shelving units, and other bits and pieces salvaged from the Banff recycling center. Bold elk approach to explore the objects,

A few bold elk may lead others to overcome their fear of humans. Photograph: Rob Found.

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triggering the cameras and leaving behind a hair sample on strategically placed sticky tape. Isotopic signatures and levels of cortisol from the hair samples allow Found to explore the links between personality and diet and whether bold individuals exhibit higher stress levels.

Bold elk appear to have facilitated an uncoupling of the natural predator–prey relationship. Localized overpopulation, the loss of elk migratory behavior, and the occasional human injury are all consequences of their urbanization.

Individual differences defy prediction

Personality studies in nonhuman species have had a slow start, considering that human psychologists have studied personality for at least a century. Only over the last decade has the study of animal personality gained momentum. Personality was not totally ignored in the past: Early work was conducted on laboratory rodents, primates, dogs, and cats. Oxford University's Felicity Huntingford was ahead of her time with her personality studies of fish in the late 1970s. But why did experts until recently largely ignore the study of animal personality in the wild?

Andrew Sih, a professor at the University of California, Davis, suggests that it is perhaps because animal personality was perceived as soft science and dangerously close to the scientific sin of anthropomorphism. Animal personality studies have crept into the field of biological sciences under various monikers, including *behavioral syndromes*, *coping styles*, *animal temperament*, and *interindividual variation*.

During the 1990s, behavioral ecologists focused on optimality, an adaptationist approach predicting that organisms evolve to behave in optimal ways to maximize their evolutionary fitness. *Optimality* encompasses the idea that animals seek food, mates, and resources in the most efficient and effective way possible, continuously trading off costs and benefits. Twenty years ago, the optimality approach was quite exciting, recalls Sih. "Optimality had plenty of hypotheses to test that did not actually require or even encourage thinking about variation within species," he says. For example, in optimal foraging, the focus was on predicting the optimal diet for a particular population or species in general, rather than on emphasizing individual differences.

Much of Sih's own research had been focused on predator–prey relationships in aquatic organisms, especially salamanders. In the field and the lab, Sih was trying to figure out which behaviors were important and attempting to explain ecological patterns. Key to explaining predator–prey interactions, explains Sih, was the idea that smart prey should rarely get eaten. "But in the system I was looking at, which was larval salamanders (prey) and sunfish (predators), there were individuals that for whatever reason were just blundering out there and not actually doing the sort of smart antipredator behavior that simple optimality theory predicted they would do." These bold individuals were the ones getting eaten, explains Sih, so the path to studying personality was a trail of understanding why prey were not always hiding as much as had been predicted.

Sharing his results, Sih realized that he was onto something that was resonating with other researchers. Sih and others began thinking that what they were observing was not just noise in the data but, rather, the existence of entire behavioral types: individuals that were too bold or too cautious in some environments, yet were doing well in others. Consistently aggressive individuals, for example, might be overly aggressive toward offspring, mates, or even predators, with potentially fatal consequences. Cautious individuals might be overly cautious, resulting in missed opportunities in safer situations. Sih and others were intrigued by the apparent conundrum of why individual animals behave consistently across different situations, given the clear advantages of behavioral flexibility. (See the Further reading section for more information on this and other studies.)

Further reading

Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. Journal of Animal Ecology. *http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2656.2011.01877.x/full*

Maternal effects and range expansion: A key factor in a dynamic process? Philosophical Transactions of the Royal Society B. *http://rstb.royalsocietypublishing.org/content/364/1520/1075.abstract*

Lovers and fighters in sleepy lizard land: Where do aggressive males fit in a social network? Animal Behaviour. *http://dx.doi.org/10.1016/j.anbehav.2011.10.028*

Personality predicts individual responsiveness to the risks of starvation and predation. Proceedings of the Royal Society B. *http://dx.doi.org/10.1098/rspb.2011.2227*

Ecological implications of behavioural syndromes. Ecology Letters. *http://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2011.01731.x/abstract*

During the late 1990s, Niels Dingemanse began his PhD at the Netherlands Institute for Ecology, in Heteren, investigating individual differences in great tits (*Parus major*), a bird species related to the North American chickadee. Dingemanse and his colleagues investigated the consistency of individual personality. During the winter, they tested exploratory behavior in this species and related this trait in young birds to their later reproductive performance and survival. "One of the most exciting results," explains Dingemanse, "was that in certain years, very bold individuals would do well, but in other years, the more shy types would do well." It was evidence for a phenomenon known as *fluctuating selection*. "It was one of the first demonstrations that no one single type always does best," says Dingemanse.

John Quinn, a professor at University College Cork, in Ireland, and a collaborator of Dingemanse's, also measures exploratory behavior in this small songbird. Taking wild-caught birds into captivity, he tests their behavior in a room they have not seen before. In this novel environment, the range of exploratory behaviors

observed is quite extreme. "Some individuals fly into one of our fake little trees and they sit there and do nothing else," he explains. "Others will go in and constantly move around the room for the full eight minutes, flying from tree to tree, exploring every nook and cranny." If those same individuals are caught a year later, they tend to do the same thing, says Quinn, which suggests that it is because of a consistent personality trait. "This trait of exploration behavior is interesting because it's heritable," says Quinn, meaning that natural selection can act on it, so it can evolve.

Dingemanse, now a professor at the Ludwig Maximilians University of Munich and also leading a research group at Germany's Max Planck Institute for Ornithology, has recently demonstrated that personality differences are not unique to one isolated population. He and his collaborators, including Quinn, compared variation in personality within four populations of great tits in the Netherlands, Belgium, and the United Kingdom. The personality differences within each population, indicated by the range of observed exploration behavior, were ubiquitous.

Timidity can be a virtue

Many animal personality studies have converged on a common measure known as the *shy–bold continuum*. At one extreme are bold individuals who are relatively fearless of novel objects and new situations. At the other extreme are shy individuals, like the great tits in the experiment that never left their perch or elk too timid to approach the unfamiliar objects. In many organisms, bold individuals also tend to be more aggressive toward others. But not always. Even within the same species, the relationship appears to vary in intriguing ways.

Sih and colleague Alison Bell from the University of Illinois set out to test whether the relationship between aggression and boldness might be context dependent. They suspected that a specific environment, such as a dangerous, predator-rich one, could induce a correlation between boldness and aggressiveness in sticklebacks (*Gasterosteus aculeatus*), a small stream-dwelling fish whose populations, Bell already knew, varied behaviorally, depending on their habitat.

Bell and Sih first tested each fish for its boldness—its willingness to look for food in a situation it might perceive to be dangerous—with a simulated predator strike by a fake great egret skull dipped into the water as the unsuspecting fish approached its food. Each stickleback's level of aggressiveness was then assessed by observing how much the fish approached, chased, and bit a stickleback intruder. Bell and Sih subsequently subjected sticklebacks to predation by rainbow trout. Once half of the sticklebacks had been gobbled up, the trout were removed, and the sticklebacks were again tested for boldness and aggressiveness. Before the experiment, there was no relationship between boldness and aggressiveness. After the experiment, the boldest fish were also the most aggressive.

Examining survival and how the boldness–aggressiveness relationship changed in each fish, Bell and Sih determined that both selection and behavioral flexibility (plasticity) were contributing factors. As for why, it is not yet clear. Bell suggests that it is perhaps because different individuals in dangerous environments have different strategies for dealing with predators. Some use *predator-inspection* behavior—a risky strategy that can involve approaching the mouth of the predatory fish to check it out. Other fish use *shoaling*—swimming in loose schools to benefit from many eyes and to reduce the risk of being eaten. "Predator inspectors tend to be loners," says Bell, "and therefore can afford to be aggressive." However, fish that shoal need to cooperate with their neighbors and to prioritize group coordination, which makes overly aggressive behavior a disadvantage. Although Bell and Sih do not yet know why predation risk induces a boldness–aggressiveness correlation, their study supports the hypothesis that correlations between certain personality traits might be adaptive in some environments but not in others.

Bell has also explored lifetime personality stability, investigating whether personality is inherited, affected by the environment, influenced by development, or influenced by a combination of factors. Fathers are sole caregivers in sticklebacks, and Bell discovered that early treatment by dads has an impact on a young fish's future personality. In an experiment in which she compared father-reared and orphaned fish, Bell found that offspring reared by attentive dads are more timid than orphans around predators. But there is much variation in parenting skills, and young fish with inattentive fathers behave no differently from those that are orphans, finds Bell. Her work suggests that early social interactions, at least in sticklebacks, are critical determinants of an individual's future personality.

Researchers found that some great tits (*Parus major*) are consistently bold and that others are timid when they are introduced to an artificial environment. Photographs: Niels Dingemanse, Max Plank Institute for Ornithology.

*The level of care provided by male sticklebacks (***Gasterosteus aculeatus***) may in uence a young fish's personality. Photograph: Tino Strauss.*

Lovers or fighters

At Flinders University in Australia, Michael Bull and his collaborators are studying the personality of lizards in relation to their social networks. With clever use of technology, Bull is investigating the social networks—not quite analogous to those on Facebook or Twitter—among group-living organisms. Bull has investigated behavior for more than three decades, studying monogamy—a relatively uncommon mating system among lizards. In the large, slow-moving species aptly called the sleepy lizard (*Tiliqua rugosa*), Bull noticed that some pairs were "like Romeo and Juliet; they were always together," whereas in other pairs, the males were "more like Tiger Woods."

Hearing about Sih's research, Bull realized that his well-studied, individually marked, and genetically pedigreed sleepy lizard population was a gold mine for personality research. With data loggers on lizards' backs to measure activity, locations, and social contacts, Bull has determined that interactions are nonrandom. "They're actually physically avoiding some of their neighbors," explains Bull. Some lizards hang out together in lizard cliques. Others are not part of the social scene. Some males are aggressive, using wide open-mouth displays and showing their impressive blue tongues. Others are meek. Examining the social network, Bull finds that the most aggressive males interact with other males but with few females, whereas the least aggressive males have more female contacts. "So we can divide this population up into the lovers and the fighters. Females avoid aggressive males like the plague," says Bull, so their personality affects their social network.

*Sleepy lizards (***Tiliqua rugosa***), found in South Australia, exhibit a range of personality types when it comes to social networks and mating. Photograph: Robin Jay.*

The methodology of Bull and his collaborators also sheds light on how personality affects the transmission of parasites and disease. By examining exactly who comes into contact with whom by means of location dataloggers, researchers can get a better idea of how the personality traits of individuals contribute to disease transmission, since disease-transmission behaviors can be difficult to observe directly in wildlife.

Also on the leading edge of personality research, in more ways than one, is the University of Arizona's Renée Duckworth. Examining geographic range expansion, Duckworth has uncovered a link between the aggressiveness of individual western bluebirds (*Sialia mexicana*) and their ability to outcompete closely related mountain bluebirds (*Sialia currucoides*). The former have undergone a 40-year trend of North American range expansion. Experimentally setting up new habitat for this cavity-nesting species by placing nest boxes in areas with no natural cavities, Duckworth quantified the aggressiveness of new colonizers. No matter where the populations were located, she found that the early colonizers tended to have more aggressive personalities.

When western bluebirds first colonize new areas, males that are highly aggressive dispersers acquire huge territories, Duckworth and her collaborators found. Her work has shown that more aggressive males have an advantage over nonaggressive males in competition for territories. But these male bullies invest little in parental care. When population density is low, the breeding success of these recently arrived male dispersers is reasonably good, but as density increases, the fecundity of aggressive males declines rapidly. In more established parts of the range, males benefit more from being nonaggressive, staying at home, and setting up shop near the parental nest box where they hatched. So in the population or species as a whole, both phases appear to be necessary, which suggests another case of fluctuating selection.

***Only when territory is plentiful do male western bluebirds (*Sialia mexicana*) that are aggressive have high levels of breeding success. Photograph: Alex Badyaev,* http://tenbestphotos.com.**

How does this system of shifting personalities work? "We see this really rapid shift in aggression once new areas are colonized, and we think that maternal effects might play a strong role," says Duckworth. Her recent work suggests that by manipulating the laying order of female and male eggs in the nest, mother bluebirds can influence their sons' aggressiveness. Moms might be playing an important role: producing sons well adapted to stay close to home when nesting sites are abundant and producing aggressive males better at dispersing when nest sites are limited. Although Duckworth's work is focused on a native species undergoing range expansion, better understanding the role of personality in invasive species may one day provide fruitful strategies for their control.

In evolutionary psychology, there is a longstanding debate about whether consistent personality precludes behavioral plasticity. New approaches in which the behavior of an individual is measured over a range of environmental conditions (reaction norms) rather than as a single data point demonstrate that plasticity and personality are not mutually exclusive phenomena. Behavioral plasticity is essential because our environment is changing frequently, explains Dingemanse, using a human example. "If it's a warm day, we take off some of our clothes, and that represents our ability of adaptive plasticity. At the same time, it might be beneficial to behave predictably. And both biological patterns are adaptive."

Back in Banff, national park staff members are testing aversive conditioning to help problematic "townie" elk regain their fear of humans. Experimentally targeting retraining efforts toward the boldest individuals, Found hopes that what he learns may help wildlife managers to restore a more natural order, reconnecting the predator–prey system. By better understanding the role of personality and by recognizing that it complements rather than replaces the role of behavioral flexibility in animals, researchers are contributing to a dynamic, exciting, and rapidly evolving field of study. Will the meek inherit the earth, or will it be the bold? If insights from animal personality are anything to go by, the answer is not quite so simple.

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