

Strong Personalities Can Pose Problems in the Mating Game

A closer look at confrontational behavior in various animals shows that aggression may help individuals survive, but it can impair reproductive success

For male fishing spiders, courtship is dangerous business. Females of the species are notoriously aggressive, and the male—which signals his arrival by gently tapping the surface of the water—often ends up as a meal rather than a mate. Yet each time the female eats her would-be partner, she lessens her chance of reproducing, leaving evolutionary biologists wondering just why this behavior persists. Aggressive female spiders just can't stop themselves, says J. Chadwick Johnson, a behavioral ecologist at the University of Toronto, Scarborough.

Johnson is among a small group of researchers investigating the “personalities” of animals from spiders and fish to insects and birds. Although many biologists once strongly protested attributing human qualities such as personalities to animals, more and more investigators are adopting such descriptive language. Individual animals, even simple invertebrates, do have consistent behavioral quirks that endow them with discernible dispositions, says Andrew Sih, a behavioral ecologist at the University of California, Davis.

Although he and his colleagues think of these dispositions as personalities, they have tried to steer clear of being criticized as anthropomorphic by instead coining the term “behavior syndromes.” In addition to identifying such syndromes in animals, Sih, Johnson, and several other investigators are finding that animal personality traits, such as being bold toward potential predators or aggressive toward cohorts, can have drawbacks, despite the traits' apparent value, say in hunting or defending territories. For example, Renee Duckworth of Duke University in Durham, North Carolina, has shown how one bluebird species' aggressiveness allows it to steal habitat from another—yet that same trait impairs the bird's reproductive fitness in certain conditions. Looking at animal personalities, and the good and bad they bring, represents “an important paradigm shift in our approach to the evolution of behaviors,” says Duckworth.

Dangerous liaisons

Many researchers credit Sih for bringing to prominence the idea that animal personalities carry survival risks. The notion plays off a proposal made 25 years ago by the late pale-



Eight-legged dominatrix. A female fishing spider devours her suitor.

ontologist Steven J. Gould and geneticist Richard Lewontin, both from Harvard. At that time, the two stirred up the evolutionary biology community by arguing that maladaptive traits could persist if they were linked with beneficial ones in an often-precarious balancing act. For example, guppies living around predators reproduce as early as possible so as to pass on their genes before being eaten. But the eggs slow gravid females down, making them easier prey earlier in life, a finding that lent credibility to Gould and Lewontin's idea.

Now, by showing that a personality trait that is counterproductive in one context perseveres because of its utility in another, Sih is moving Gould and Lewontin's ideas “into a new arena,” says evolutionary ecologist

Andrew Hendry of McGill University in Montreal, Canada. Sih argues that because some animals are very limited in their ability to moderate their personalities according to particular situations, they are stuck with the consequences throughout their daily lives.

Take the North American fishing spider, the subject of Johnson's studies. In 1997, Göran Arnqvist of Uppsala University in Sweden and a colleague suggested that aggressive females who eat males who come courting were simply following their strong instincts to catch prey. The drive to hunt would serve juvenile females quite well, enhancing their growth, particularly when competition for food was intense. But those instincts, if unfettered, may backfire when the females become adults and need mates.

Johnson has recently followed up on this proposal, verifying key elements. He found that even as young spiders, certain females were aggressive hunters, spending more time than their cohorts searching for the next meal and, as a result, bulking up more. This aggressiveness was also reflected as boldness in encounters with predators, Johnson discovered when he mimicked a bird's approach by tapping the water near these spiders. Although all fishing spiders dove into the water when they detected such tapping, the female superpredators surfaced more quickly.

These daredevils also were more likely than less aggressive females to try to snack on males, Johnson reported last month at Evolution 2005 in Fairbanks, Alaska. “Boldness to a simulated predator is proportional to the tendency to attack males,” he said. Overall, he concluded, the bold, aggressive female spiders ate more food, but they compromised their survival and productivity by treating males as food and taking predation risk lightly.



No love lost. A female water strider struggles to get a male off her back.

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Daniel Promislow of the University of Georgia, Athens, is surprised that aggression can pervade all aspects of a female spider's life. If the fishing spiders could modulate their personality, he explains, then the females should be as aggressive as possible in hunting, less aggressive in the face of danger, and mild-mannered when approached by males—but that's not what the experiments indicate. "We often think of behaviors as relatively plastic traits compared to morphology, physiology, or life history," he says, but Johnson's results challenge that premise.

Counterproductive aggression is not limited to female arachnids. Sih has found that militant males are the troublemakers among insects known as water striders. Sih graded aggressive tendencies in males by observing, for example, how much they fight, how long they were active, and how often they chased after potential female mates. He then put together 12 groups of water striders, each consisting of males with similar personalities from least aggressive to most aggressive, in separate artificial ponds. The researchers then put females into the ponds and monitored each group's mating successes and failures, keeping track of each individual's partners within their group. The investigators also tracked each water strider's feeding and tallied how often an individual retreated to riffles, supposedly a more dangerous habitat but also a refuge from aggressive peers.

Females tended to avoid the most aggressive males, the researchers found. Indeed, females often refused to put up with any "Rambo" male in their midst and moved as far away from him as they could, diminishing both his and his peers' mating opportunities. Aggressive individuals couldn't turn down their swagger. They ultimately "hurt not only themselves but, by being too aggressive, the entire group," Sih reported at the evolution meeting.

Group dynamics

Working with small fishes called three-spined sticklebacks, Alison Bell of the University of Glasgow, Scotland, has found that living conditions may narrow the range of personalities within a group of animals. Whereas researchers such as Sih and Johnson typically focus on the behavior of individuals in a population, she is assessing variation in "in your face" behavior—the combination of boldness and aggression—between and within whole populations of the fish. Because stickleback populations have diverged genetically, so might their behavior in different places, she hypothesized.

To examine this possibility, Bell collected groups of 20 juveniles from 13 different populations of freshwater and marine



Buzz off. A test of aggression shows that western bluebirds are quite fierce against swallows.

sticklebacks in various lochs and harbors around Scotland. Some of these populations regularly faced predators—pike, trout, and the like—and others lived in relatively predator-free environments. To measure boldness of the fish from each population, she set up a tank with a pike behind a glass divider, then counted how often individual fish approached the pike to inspect it. For a gauge of aggressiveness, she counted the number times a fish isolated in one tank tried to nip at other sticklebacks in an adjoining tank separated by glass.

The fish within each of the 13 populations seemed to share similar mindsets. Bell found that when one individual from a population fearlessly approached the pike, so did most of the others from those groups. In general, most of the fish within a particular group acted the same way, she reported. And fish from the boldest populations, as measured by the pike test, were also the most confrontational toward other sticklebacks. In the wild, says Bell, this bullying could translate into bigger territories, better food, and even increased mating for the biggest bully. But the fearlessness toward predators may also cost fish in these aggressive groups their lives, suggesting that whole groups of animals, not just individual ones, can have personality traits that threaten reproductive success at times.

Bell also observed that the bold, aggressive stickleback populations had higher breathing rates, more spines, and heavier body armor than more wimpy populations. Those correlations suggest that "behavioral syndromes might be part of a larger package of evolutionary [traits]," says Sih.

Duckworth's studies indicate that sometimes the bold personality of one species can help it beat out similar, but shyer, species, at

least in a particular environment. Observations over the past 40 years show that western bluebirds have greatly expanded their range in Montana, displacing mountain bluebirds. By tallying the number of each bluebird in places where both species are present, Duckworth documented that western bluebirds in just a few years supplanted mountain bluebirds at valley study sites. Much of the western bluebird's success sprang from its fierceness, suggests Duckworth.

She placed tree swallows, a bluebird competitor, in nest boxes, and then watched as either of the bluebird species approached the box. She found that western bluebirds were more aggressive, an indication that they are better able to acquire and defend their territories against the swallows. The male western bluebirds also were fiercer than mountain bluebirds when competing for mates, another sign of pushy temperaments.

In this case, aggressiveness seems to go hand in hand with reproductive success. But a closer look suggests that, as with fishing spiders and water striders, the western bluebird's obnoxiousness can come with a cost. Duckworth points out that western bluebirds spend so much time defending their nests and courting that they neglect their offspring. This poor parental behavior is especially problematic in tough environments, such as mountains. In contrast, mountain bluebirds are loyal parents and have an edge where weather can be rough, says Duckworth. As a result, they have maintained their foothold in Montana's mountains. "Behavioral syndromes can have profound ecological and evolutionary consequences by mediating species coexistence," Duckworth says. Thus, in animals, as in people, personality can make or break one's success in life.

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