

The Evolution of Risk-Taking

By Lee Alan Dugatkin, Ph.D.

Editor's note: Many animal species besides humans show evidence of individuality. Knowing how a risk-taker differs from its stay-at-home counterpart could not only help humans live more easily with our fellow creatures, says Lee Dugatkin of the University of Louisville, but also tell us a few things about ourselves and how we got this way.

I'm going to make the case that we can study the evolution of risk-taking by closely examining work on this subject in nonhumans. Researchers have found several ways to study behavior and emotion in animals. Sound fishy? Here's a beautiful example of how it is done.

Psychologists use a suite of measures to assess what they call "subjective well-being": a composite well-being score is assigned to you after others rate you on how happy you appear to be. Ethologists, scientists who study animal behavior, recently modified the scale to apply it to orangutans. Alexander Weiss and his team found two general types of orangutans residing in zoo populations. One type, which seemed happy and outgoing, interacted in positive ways with other apes and with their zookeepers and rarely showed abnormal or neurotic behavior. The second type showed the opposite set of traits (Weiss et al. 2006).

So far, so good. But does what Weiss's team found translate in any real way to what we mean by the common usage of "happy and well-adjusted"? It does in

orangutans: The apes that the Weiss group scored high on the well-being scale lived far longer. Orangutans that were one standard deviation above the group norm for subjective well-being lived about 11 years longer than did their subjectively less happy group mates, which were one standard deviation below the group mean.

If we can study subjective well-being in nonhumans, then, in principle, we can study risk-taking as well. And there is every reason we'd want to do that. In humans, risk-taking, often referred to as boldness, is one of the most consistent personality traits displayed over the course of an individual's lifetime. The same is true for the other end of the continuum, risk aversion (which overlaps, but is not synonymous, with shyness). And psychologists, perhaps most notably Jerome Kagan, have done wonderful work on risk-taking and shyness in humans. But there are limitations (Kagan 1994). Ethologists point out that, from an evolutionary perspective, research on humans is lacking for at least two reasons. First, at the species level, humans are a sample size of one. Second, we don't know much about the costs and benefits of risk-taking in natural settings, but it is knowledge of the costs and benefits of a behavior that allows us to use natural-selection thinking to understand evolutionary history and to make predictions about the future. We could remedy both problems by looking at the costs and benefits of risk-taking across many species. And that is what we have started to do.

Curious Fish

One of the earliest controlled ethological studies of risk-taking began in the experimental ponds at Cornell University, where David Sloan Wilson and his colleagues began searching for different personality types in the pumpkinseed sunfish (*Lepomis gibbosus*). Based on work in humans, Wilson and his team hypothesized that risk-taking sunfish would be especially likely to explore novel objects and novel environments (Wilson et al. 1993; Wilson et al. 1994). They collected fish from a pond with a series of funnel-shaped traps designed so that if a fish swam into one, it was very hard to swim back out. Presumably, risk-taking fish would be more likely to explore such a novel trap, and the researchers would catch more risk-taking fish than risk-averse fish. The researchers also dragged a large net through the pond and scooped up all the fish they could, both bold and shy. If Wilson and his team were correct, the fish from the funnel traps would be bolder on average than those from the netted samples.

Wilson's found that pumpkinseed populations are mixtures of bold and shy fish. For example, stomach-content analysis indicated that fish caught in the funnel traps had been eating more often and in areas of the pond that were the least safe—the sorts of behaviors that we might expect from risk-taking individuals. Funnel-trapped fish also had many more parasites than did netted fish, suggesting that they explored many areas of their pond and thus exposed themselves to myriad parasites.

When funnel-trapped and netted fish were marked individually with colored beads and released back into their pond, funnel-trapped fish were much more likely

to be found leaving their group and foraging on their own than were net-trapped fish. And, finally, when pumpkinseed fish were brought into the laboratory and exposed to a novel object there, funnel-trapped individuals were much more likely to investigate the object. These results suggest that, just as in humans, a continuum of risk-taking propensities exists in nonhumans.

Let's switch species. Since I was in graduate school, I have been fascinated—"obsessed" might be a better word—with what is called predator inspection behavior in the guppy (*Poecilia reticulata*). Predator inspection is akin to military guard duty. One or a few fish break away from the safety of their group and slowly approach a potential predator to gather information about its possible danger. At first, my interest in predator inspection focused on the cooperative nature of the ways that pairs of fish inspected—ways that matched predictions from economic models of cooperation. But then I realized that predator inspection would also allow me to measure the costs and benefits of risk-taking. After all, I was finding that some fish were consistently willing to take the risk of inspecting predators, while other guppies consistently avoided such risky behaviors. Why? What were the underlying costs and benefits that drove the evolution of risk-taking in this system?

The cost of predation inspection was fairly easy to measure and arguably intuitive. If you take risks in the presence of a predator, you get eaten more often—and indeed, controlled experimental work, in which groups with different numbers of risk-takers were monitored, confirmed that risk-takers are more likely to end up in the guts of predators (Dugatkin 1992). Measuring the benefits of predator

inspection behavior proved to be more conceptually challenging. What were the guppies getting out of these risky endeavors? For natural selection to favor *any* amount of predator inspection behavior, there must be compensating benefits for undertaking this risky behavior, but what are they? My colleague Jean-Guy Godin had a clue when we saw something unexpected. Much research had already demonstrated that female guppies generally prefer more colorful males as mates. What we were seeing was that more colorful males also tended to be risk-takers (Godin and Dugatkin 1996).

We ran a series of experiments designed to see if it was a male's color, his risk-taking tendencies, or both that made him attractive as a potential mate to females. When we experimentally decoupled boldness and color (using a nifty experimental device that a former engineer at NASA built for us), female preference was most directly linked to risk-taking behavior in males. Why females prefer bolder males is still not understood, but it may be that boldness is a signal of genetic quality. What does seem clear is that natural selection has favored males that temper their risk-taking behavior as a function of the benefits available: Colorful males inspect predators far less often when females are not watching them than when females are observing what they do in the presence of a predator.

Attraction to the opposite sex may not be the only good thing to come from risky bouts of predator inspection. My colleague Michael Alfieri and I also found that risk-takers were better at learning associative-memory tasks than were risk-averse fish. We measured a guppy's tendency to inspect predators and, in a separate test,

its ability to pair food with an arbitrary cue. Bolder guppies learned this associative-learning task more quickly than did their shyer group mates (Dugatkin and Alfieri 2003). But there is an interesting catch here: Bold fish were better learners *only* after they had recently expressed their boldness. Why this is so is an area ripe for future exploration.

Birds of a feather

Over the last two decades, Peter Drent and his colleagues have been studying risk-taking in the great tit bird (*Parus major*). Two overarching personality types emerge in this species. “Fast” birds explore new environments with rapid-fire speed and are quite aggressive. They are the risk-takers. “Slow” birds show the opposite behavior pattern. In a clever experiment involving “tutors,” the researchers also found that fast birds would switch habitats when a so-called tutor passed on information that a new habitat was profitable, but slow birds, which spent more time focused on their environment and less on the tutors, paid less attention to tutors (Marchetti and Drent 2000).

Drent and his team followed birds in natural populations with an eye toward studying the mating patterns of fast and slow birds. They found that fast birds that mate with fast birds and slow birds that mate with slow birds are the pairings that produce the most offspring (Both et al. 2005). These researchers have even gone so far as to create experimental “lines” of great tit birds, by mating the fastest birds

with the fastest and the slowest with the slowest. They then examine how genetics and development interact to shape personality (Naguib et al. 2011). This work, in conjunction with other studies, shows a clear genetic basis to risk-taking personality traits in this species.

Including the orangutans at the opening of this piece, we have looked at personality in mammals, fish, and birds. But some researchers have argued, and rightly so, that this is a very vertebrate-centered view of personality, and that invertebrates may also have much to teach us about the evolution of risk-taking and personality. Work in this area is scant, but studies on red octopuses (*Octopus rubescens*) and dumpling squid (*Euprymna tasmanica*) have uncovered evidence that they, too, show a bold-shy continuum (Mather 2008; Sinn et al. 2010). One especially appealing aspect of future work in invertebrates is that the nervous system of cephalopods, like octopuses and squids, is both well understood and easy to study (cephalopods are famous in neurobiology for their giant neurons), thus allowing potential insight into the underlying neurophysiology of risk-taking.

Applications Near and Far

The study of risk-taking behavior has practical, as well as conceptual, value. For example, conservation biologists have had some success at reintroducing large carnivores, like wolves, into their native habitats. Though these programs should be applauded, they sometimes have unexpected negative consequences, such as the rekindling of old rivalries between the conservation biologists implementing these programs and ranchers who keep domesticated animals on which the reintroduced

large carnivores feed. Research on animal personalities might help reduce such tensions.

More specifically, there is mounting evidence that much of the hunting of domesticated animals by wild carnivores is done by a small number of “problem individuals”—that is, the same individuals repeatedly attack and kill ranchers’ livestock. Studies of hunting behavior in wolves, cougars, leopards, seals, lions, tigers, bears, and other species all hint at the presence of such “repeat offenders.” Attacking ranchers’ livestock carries high risk: A predator must first circumvent any fencing or other defensive measures put into place and then risk being shot by ranchers. Predators that consistently attempt to attack such livestock display many of the personality traits associated with boldness (Dugatkin 2009).

Suppose we stop thinking in terms of “repeat offenders” and instead focus on measurable characteristics like boldness. We might examine whether bold predators use particular paths to reach prey, hunt at particular times, or are more or less attracted to certain stimuli than risk-averse predators are. Then, rather than shooting “problem individuals,” perhaps wildlife workers could build traps tailored to the hunting strategy of bold predators. Understanding the science of risk-taking might help spare the lives of these carnivores, while at the same time helping ranchers protect their stock.

Another practical application of work on animal personalities centers on the use of animals to aid disabled people. To become a guide for blind people, for example, dogs must pass through a series of tests, and the factor that eliminates the

most dogs from the pool of possible guides is fear. Some dogs are just more frightened by novel things in their environment, and they are less willing to take risks to help the person they are guiding. Based on this phenomenon, researchers have developed a scoring system for fear and fearlessness and implemented it across dog breeds to find the breed most likely to aid blind people.

We've made some progress, but much work remains to be done on the evolution of boldness in animals. We need a better understanding of the molecular genetics and the underlying neurobiology and endocrinology of this trait. We need mathematical models of risk-taking; these models are only just emerging in the growing animal literature on behavioral syndromes. We need a deeper understanding of the phylogenetic—that is, evolutionary—history of boldness. Almost nothing is known about this, though Alexander Weiss has some fascinating ideas about the relationship between the evolution of personality traits in humans and that of our closest living relatives (Weiss et al. 2011).

I'm optimistic on all fronts. The more species we investigate, the more costs and benefits we measure, the more theory we develop, and the more new tools we develop to study the genetics, neurobiology, and hormonal underpinnings of boldness, the better we will understand boldness in nonhumans and, eventually, humans.

Citations

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