Fear Factor

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The surprising consequences of being scared

Radio signals suggested that the lions were on the move. So 22-year-old Alayne Cotterill moved faster. Tracking the carnivores on foot in Zimbabwe, she broke into a jog. As she burst into a clearing in the woodland savanna, she discovered that she was standing at the guts of a kill. "There was this jagged rib cage sticking up in front of me, with all the lions right there, just staring at me," she recalls. The seven lions jumped back a few feet and kept their gaze on Cotterill. Her heart was racing.

Although she was completely unarmed, the lions ambled off, leaving the carcass behind. Disturbing their dinner had been unintentional, "but it was a rather graphic example of how hardwired a fear of humans is, for most lions," says Cotterill.

Her more recent research into human–lion conflict investigates how fear of death at the hands of humans affects the behavior and space use of top carnivores. Now, she is applying that knowledge to inform decision-making in lion habitat conservation, aiming for what she and her colleagues have called a "Landscape of Coexistence" for large carnivores that are feared by their prey—but that also fear us.

With even top carnivores making decisions influenced by the fear of death, scientists are finding fresh evidence that fear is a critical factor in how individuals behave and even how ecosystems function. Fear ecology is now a thriving research area—a fascinating new field with old roots.

Fear of wolves, not just their direct killing of prey, appears to have cascading effects on their entire ecosystem. Photograph: C. Darimont, raincoast.org.

The roots of fear ecology

Predators are not always successful in pursuit of prey. Prey often escapes, providing an opportunity to learn from near-death experiences. The idea that animals would behave and distribute themselves according to a "landscape of fear" was conceptualized as a three-dimensional spatial representation of fear combining the physical coordinates of an area with the level of predation risk in a 2010 paper by John Laundré (www.cof.orst.edu/leopold/papers/Laundre_etal2010.pdf) at the State University of New York, with colleagues at Oregon State University. It drew on earlier work by him and others, such as Altendorf and colleagues, in 2001.

But the roots of fear ecology can be traced much earlier still to predator–prey studies, such as those looking at moose behavior in the presence of wolves.

In 1990, Steven Lima and Larry Dill, then at Simon Fraser University, in Burnaby, British Columbia, published a review of the state of knowledge of behavioral decisions made under the risk of predation. At the time, the field was about 10 years old, says Lima, and "it was an opportune time to bring it all together." He published another review of the growing research area in *BioScience* in 1998 (doi:10.2307/1313225).

In the 1990s, Lima was one of many behavioral scientists recognizing that

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"getting killed was a hell of a lot worse than losing a meal" and that the nonlethal effects of predation could be more important than was previously realized. Fear ecology as an area of research emerged, in part, from behavioral ecology studies of optimal foraging—how animals make decisions about what, where, and when to eat. Lima, now at Indiana State University, and others thought that incorporating predator–prey dynamics could advance foraging ecology further.

One engine that stimulated interest in the ecological implications of fear was the Kluane Boreal Forest Ecosystem Project, a long-term study of snowshoe hares in Canada's southwest Yukon. Co-led by Charles Krebs, an ecologist now retired from the University of British Columbia (UBC), Canadian ecologists divided the forested habitat into square-kilometer blocks and compared unaltered control sites with those that had experimental additions of food and the removal of predator access via fences. What they documented (*http://faculty.weber.edu/jcavitt/Krebs.pdf*) was that food supplementation tripled the number of snowshoe hares produced on the nonsupplemented sites. And in blocks where predators such as lynx were excluded, hare numbers were double those in squares where predators were not excluded.

What the researchers expected, if the processes were simply additive, was that by combining food supplementation and predator exclusion, there would be five or six times as many hares. Instead, under these safer, food-rich conditions, they found 11 times as many. The results pointed to food and predators interacting as synergistic effects, with "some other thing—behavioral, physiological, or psychological—that's mediating their ability to take advantage of the resource," says Michael Clinchy, adjunct professor at the University of Victoria.

In short, "scared prey eat less," explains Liana Zanette, who studies fear at Western University. "Behaviorally, everybody knows that animals drop what they do whenever there's a predator around and attend to the predator," she explains. "But that's at the expense of other things, like eating."

Liana Zanette and her team studied what happened to the behavior and diet choice of coastal raccoons in an experiment in which the sounds of barking dogs brought fear of predators back into their community. Photograph: Michael Clinchy.

Population ecologists have traditionally thought about biological communities as having a "top-down" or "bottom-up" structure. Top-down communities are structured from the top of the food chain. The classic example is the sea otter. As top predator, it keeps sea urchins in check, allowing all of the diversity of life in a kelp forest to flourish. Bottom-up communities are structured by the availability of plant food—such as grass for grazing herbivores on the African savanna. What Zanette studies "integrates those two ideas," she says.

In the Gulf Islands of British Columbia, in the early 2000s, Zanette and her colleagues, including the late James Smith at UBC, studied the dual effects of food and predation on the breeding success of song sparrows. In the experiment, song sparrows in the low-predator environment did 50 percent better. When the researchers added food to the high-predator environment, birds did 50 percent better. So if the factors were additive, they expected that when they added food to the low-predator environment, the birds would do 100 percent better. Instead, the combined effects of added food and lower predation meant birds had 200 percent better breeding success, with synergistic effects, just as with the snowshoe hares.

From song sparrows to sticklebacks and salamanders

That finding sparked Zanette's interest in quantifying the effect of predator fear alone. To do so, Zanette and her team experimentally removed actual predation. To protect song sparrow nests, they used electric fences and netting so that predation was reduced to zero. Then, they manipulated perceived predation by using playbacks of recorded predator sounds, hanging loudspeakers from trees. To one cohort of sparrows, they broadcast a suite of 12 different predator calls, including owls' and raccoons', to see how the sparrows would respond. To another group of sparrows, they played nonpredator calls. Nonpredator calls had frequency characteristics similar to those of the predator calls—matching raven caw with goose honk, for example.

In this experiment, published in *Science* in 2011, Zanette and collaborators discovered that sparrows protected from actual predation but scared by predator calls produced 40 percent fewer offspring over the season. Cameras were used to confirm that no actual predation occurred. "So we know there is no direct predation. This is just terror," says Clinchy.

Mothers who heard the predator calls were "really skittish," says Zanette. They also laid fewer eggs, incubated less, had lower hatching success, and fed their babies less often, so more of their young starved as compared with the sparrows played the nonpredator calls. But the effects went further, permanently disadvantaging the surviving young. The surviving sons of the predator-sound-scared parents also had a more limited song repertoire when they grew up to be adult males themselves. What is sexy to female song sparrows is the diversity of songs that a male can sing. This affects a male song sparrow's lifetime reproductive success. What Zanette's team found was an intergenerational effect of fear: Scared song sparrow parents may pass on their lower likelihood of reproductive success to subsequent generations through their song-reduced sons.

The transgenerational effects of fear have also been studied in stickleback fish, with work by Alison Bell at the University of Illinois, Urbana-Champaign. In the natural habitats where these small fish live, "everybody loves to eat sticklebacks," says Bell. Predation is their main source of mortality. Bell has long been intrigued by behavioral variation among individual sticklebacks in the presence of predators. In January 2016, Bell shared her work in a session on the genetics and neurobiology of fear at the Gordon Research Conference held in Ventura, California, on predator–prey interactions, part of a conference series created by Zanette, Clinchy, and Rhode Island University's Evan Preisser.

Song sparrow nestlings in their nest. Liana Zanette and her colleagues removed actual predation and studied song sparrow response when only the sounds of predators were heard. Photograph: M. C. Allen.

Researchers Aija White and Marek Allen erect a temporary electric fence to protect song sparrow nests from predators. Research has shown that song sparrows protected from real predators but scared by their sounds have 40 percent fewer offspring than their less fearful counterparts. Photograph: Liana Y. Zanette.

Bell and Katie McGhee, a postdoc in the lab who is now at Sewanee University, investigated how the nonlethal effects of predators on stickleback parents transfer to their offspring. It is work inspired by research on zebra finches in the late 1990s and early 2000s that revealed that mother birds can influence the quantities of steroids incorporated into their eggs, shaping the development of their young. Bell knew from previous research that adult fish mount a cortisol response to predation, producing stress hormones when they are around predators. Bell wanted to find out whether this affected the next generation, so her lab conducted an experiment in which gravid females were exposed to unpredictable cues of predation. "We would come in with a model predator and chase them around the tank," says Bell. They repeated these scare tactics daily with ecologically relevant predators, such as model pike or model sculpin, until the female was ready to spawn. Then, they compared the eggs and offspring of these predator-chased females with those from an unchased control group. They found a variety of effects. Fear treatments affected offspring metabolism, learning, schooling behavior, survival in the presence of a predator, and gene expression. There were "tons and tons of consequences," says Bell.

Cortisol seemed like the obvious mechanism, so Ryan Paitz, another postdoc in Bell's lab, tested its effects. Stickleback embryos did take up cortisol from the environment, as the team discovered via radioactive tracing studies. But within three days, "embryos seemed to be able to kick the cortisol back out of the egg" without metabolizing it, Bell says. So in sticklebacks, at least, the mechanism for the delivery of the fearful "message" about predation risk remains an enigma. Her lab is investigating whether these danger messages might be communicated via microRNA.

A wealth of mammalian research also suggests that maternal stress, such as fear of predators, has negative effects on offspring cognition. Bell and McGhee have found evidence for this, too. In their experiments, individual offspring of predator-exposed sticklebacks took longer to learn color-discrimination tasks. But when they looked at learning in groups of six, they found something intriguing. The "offspring of predator-exposed moms really quickly learned to follow the leader," says Bell. That meant that even though the first fish in the group took a long time to figure out the learning task, the "learning-cloud" environment meant that each subsequent fish in the group learned more quickly, with the net effect being that the experimental group, as a whole, was no slower than the control group.

Stickleback fear can be transmitted across generations, via mechanisms being investigated by Alison Bell and her colleagues. Shown here is a gravid female stickleback. Photograph: Katie E. McGhee.

"If you read the biomedical literature about maternal stress," says Bell, "they'll tell you it's horrible," referring to the many documented detrimental effects on offspring, including cognitive deficits. But in the behavioral ecology world, theory and data suggest that animals can adaptively prepare their offspring for living in a high-risk environment. Bell's research has revealed both adaptive and harmful nonlethal effects of predators, suggesting that the answer to whether fear is always a bad thing is "it depends."

One group in which the adaptive transgenerational effects of fear have been well studied is amphibians. Some salamanders and frogs, for example, appear to be able to customize their knowledge of predators to their environment, beginning in an embryonic state. This is one of the research areas of Alicia Mathis at Missouri State University. In the ringed salamanders (*Ambystoma annulatum*) she has studied, adults are terrestrial and find temporary ponds in which to breed and lay eggs. Eggs hatch into aquatic free-swimming larvae and then metamorphose into terrestrial juveniles before growing into adults. Salamanders breed in temporary ponds that dry up every year; these ponds do not contain fish. Amphibians do well in these fish-free ponds, but there are still a whole range of predators, including aquatic insects, snakes, wading birds, and other cannibalistic salamanders. Mortality in the ponds is very high, with survival rates often as low as 10 percent or less. Because many of the predators can eat the salamanders only when they are very small, salamanders are under pressure to grow quickly and "get out there and eat, eat, eat, eat," says Mathis.

Because the water in which these young salamanders swim contains chemical clues about their environment, potentially including what other species are in the pond, Mathis was curious to find out if young can learn from these cues to guide their behavior. She and collaborators conducted an experiment to examine the response of young from eggs raised in a risky versus a safe environment. "What we wondered was whether they would be able to take advantage of all of this information they are bathing in and adjust their behavior accordingly," she says. Indeed, they did find these discrimination abilities, which appear to be so fine tuned that they allow salamanders to distinguish between fellow salamanders that have been cannibalistic—and are therefore dangerous—and noncannibalistic salamanders that are not a threat, says Mathis. Salamanders raised in riskier environments were less active and sought out shelter more frequently. Mathis's team also found that wood frog tadpoles learned to respond to chemical cues signaling the danger of unfamiliar predators. Both salamanders and frogs learn from the experiences they have while still in the egg or larval stage, she explains.

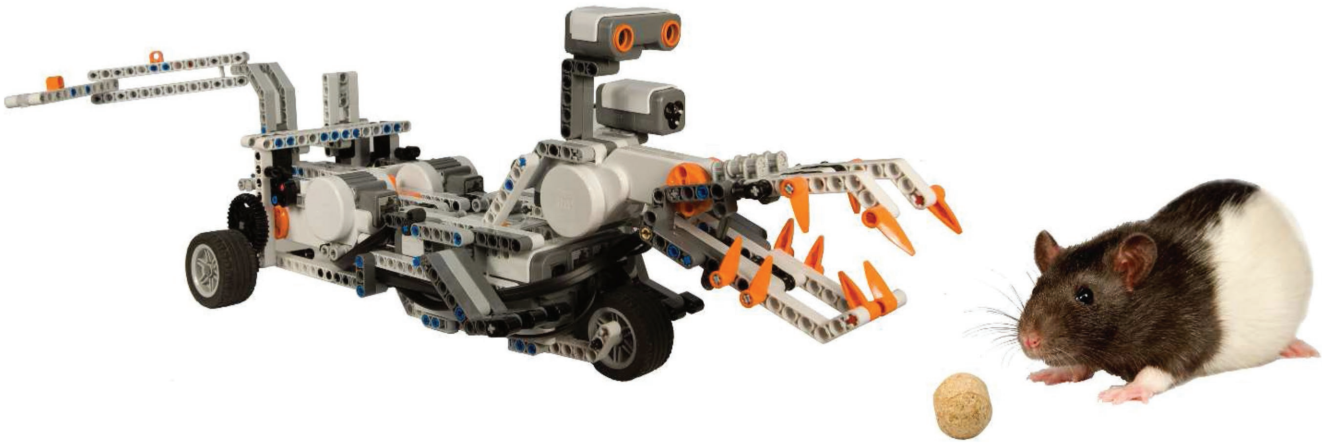
It is a discovery that Mathis is now putting to use to aid conservation in the *head starting*—the term for captive rearing followed by release—of an endangered salamander species, the hellbender. By teaching the naive larvae of this species about the kinds of things to fear by using predator-flavored water for rearing rather than water with no social cues, she may be able to increase their chances of survival when captive-raised individuals are released into the wild.

*Exposing the hellbender (***Cryptobranchus alleganiensis***), a large endangered salamander, to predator-flavored water may give captive-reared larvae a better chance of survival in the wild. Photograph: Adam Crane.*

Raccoons in British Columbia's Gulf Islands wreak havoc on intertidal communities when there are no longer predators to fear. Photograph: Michael Clinchy.

The role of fear in an ecosystem

Recently, Clinchy and Zanette found that the effects of fear go far beyond single species. In the Gulf Islands, they examined whether fear can cause a trophic cascade—the ecological equivalent of a domino effect across a whole community. Their study location was ideal because on the west side of Vancouver Island, raccoons are midlevel predators, sharing habitat



The "robogator" Jeansok Kim has used to examine the fear response of rats. Photograph courtesy of June-Seek Choi and Jeansok J. Kim.

with apex predators such as cougars, bears, and wolves. There, "wolves and cougars love to eat raccoons—they are a major prey item," says Zanette. But on the east side in the Gulf Islands, all three of these predators have been extirpated for a century, and raccoons have stepped up as ecological kingpins. The only animal these island-based raccoons fear now is the domestic dog.

As a result, Gulf Island raccoons have radically changed their habits. Usually nocturnal, these raccoons have become bold daytime hunters. "They like to eat songbirds," explains Zanette, but they also like to feast from the intertidal zone, "and you'll see them kilometers out, where there are no trees and no places to hide," she adds. As a result, Gulf Island raccoons have been hammering bird populations and a host of marine invertebrate species—from worms to crabs and snails.

Zanette and Clinchy decided to see what would happen to raccoons if an element of fear were restored. With colleagues, they broadcast dog barks from some beaches and the benign sounds of barking seals from others. What they discovered, published in *Nature Communications* in 2016, is that on barking-dog beaches (but not on barking-seal beaches), raccoons, even after a month, spent less time feasting on seafood and more time being vigilant. "It suggests that restoring the fear of predators to a landscape can mean massive benefits to an ecosystem," says Zanette. That fear can have cascading effects through communities has also sparked numerous studies—and vigorous debate—about the nonlethal impacts of the restoration of wolves to Yellowstone National Park. At the time of wolf reintroduction to the park in 1995 and 1996, elk numbers were high. Elk provided an abundance of food that allowed the wolf population to grow rapidly. As wolf numbers increased, elk numbers decreased (although their numbers were further depressed by a drought and human hunting). There is now significant evidence that elk in Yellowstone have changed their habits to feed in safer areas, where wolf ambushes are less likely. This appears to have allowed riparian vegetation such as aspen, cottonwood, and willow trees that were previously heavily browsed to recover, with knock-on effects such as an increase in bird diversity.

But it is not just ecosystems and endangered species that may benefit from better understanding the ecology of fear. There is a growing realization, spurred by increased cross-disciplinary communication at meetings such as the Gordon Conference, that ecological fear studies might help solve some of the puzzles that medical scientists are grappling with, too.

At the University of Washington, Seattle, neuroscientist Jeansok Kim explains that the "Pavlovian conditioning paradigm is probably one of the most widely used paradigms in neurobiological memory research and translational research to understand anxiety disorders in humans, such as post-traumatic stress disorders." In the Pavlovian conditioning paradigm, research animals, typically rats, are trained to associate a benign stimulus with a frightening one, such as an electric shock. Animals quickly learn to fear the benign cue because of what they have learned to expect afterwards: pain.

But about 7 years ago, Kim got an idea while picking up his son from his Lego robotics club at middle school and examining the creatures the kids had made. He was intrigued to find out what happened in the brain when lab animals were exposed to more realistic, ecologically relevant, pain-free stimuli. So his son built him a programmable Lego Mindstorms "robogator" that Kim used to examine the fear response of rats. Each hungry rat, lured to leave the safety of its nest by a food pellet, would trigger the predatory robot to surge forward and snap its jaws. In response, rats instinctively fled for the safety of their nest. Testing rat responses to the robogator placed differing distances from the food pellet, Kim learned that rats appear to form a “distance gradient of fear.”

By looking at the brain region affected, he has found that “while the amygdala seems necessary for many forms of defensive behavior, emerging evidence suggests [that] fear networks that include the hypothalamus, periaqueductal gray, and regions of the medial prefrontal cortex, among others, are distributed throughout the brain, and some may support fear responses without the amygdala.” That is the idea he and Blake Pellman outline in a recent review in *Trends in Neurosciences* (doi:10.1016/j.tins.2016.04.001), and it is important because the amygdala has long been thought to be the key brain area affected by and responding to fear. Kim has only recently begun interacting with ecologists who study fear. He is optimistic that increased interaction between these disparate disciplines may benefit both areas of research.

Nearly three decades have passed since Lima and Dill pointed out gaps in knowledge about the nonlethal effects of predation. They highlighted a lack of research on fear’s effects on reproduction, the nature of predation risk, and how animals perceive threats. Since then, much ground has been gained. Ecological fear of predation, independent of predation itself, has now been conclusively demonstrated. Now, an advancing understanding of fear as a powerful evolutionary force is shedding light on how fear affects individuals, populations, species, communities, and ecosystems, making such fearful knowledge a valuable management, conservation, and even medical tool only just beginning to be tapped.

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Further reading.

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