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photo by Tina Wey

DO MARMOTS RETAIN FEAR OF EXTINCT PREDATORS?

BY DANIEL T. BLUMSTEIN,
UNIVERSITY OF CALIFORNIA
LOS ANGELES

If you've moved to Crested Butte from a more dangerous place, how long did you continue to lock your doors, clutch your keys in your hand when walking to your car at night, or keep lights on outside your home? In other words, how long did your fear of the more dangerous place persist in our much safer community? (I live in LA and gladly shed most of my fears immediately upon coming here, but I do still lock my truck...). As a biologist, understanding the answer to this question is important because many species are now living with a subset of the predators that they've evolved with. In some cases, we're trying to reintroduce those predators and it's important to know whether these reintroductions will cause deleterious impacts on potentially naive prey.

I study yellow-bellied marmots at the Rocky Mountain Biological Laboratory in Gothic and I've been using them as a model system to gain some insights into the time course of relaxed selection on antipredator behavior.

Antipredator behaviors such as fear and anxiety are costly, and we generally expect animals to lose fear and other antipredator behaviors when they lose their predators. A classic example comes from guppies (which actually live in the wild, not just aquarium tanks). Female guppies find colorful males sexy. However, bright coloration comes with a cost—they are easily detected by predators. Guppies in locations with predatory fish are relatively more drab than those in populations without predators. Ingenious experiments found that by removing predators, there was a rapid evolutionary response whereby guppies became more colorful. Putting predators back in the system quickly reversed

this—making formerly colorful guppies drab again. Thus, guppies tell us that evolution can happen quickly, and costly antipredator behaviors or other traits (coloration in the guppies' case) are lost quickly following a relaxation of predation. But what about marmots?

Marmots used to have to worry about predation by wolves, but wolves have been extinct in Colorado since around 1940. However, a wolf was filmed near Walden, just below the Colorado-Wyoming border, in February 2007. If and when wolves re-colonize Colorado, will they find a vulnerable population of marmots? To know this, we need to know if marmots can still recognize wolves.

Marmots have a hard life: they have to avoid predation by foxes, coyotes, badgers, bears and eagles, while still eating enough to lay down sufficient fat to survive the winter. We recently discovered that marmot populations living in relatively safe places (areas with good visibility and rocks to protect them from badgers) do not go extinct, while marmots in less safe areas periodically go extinct. We also, unexpectedly, discovered that the relative amount of food did not explain extinction risk. Thus, avoiding predation not only has profound effects on the behavior of animals, it also may influence the likelihood of a population persisting over time.

My students and I have conducted a number of experiments looking at the ability of marmots to identify their extant and extinct predators and we've found that marmots retain the ability to recognize wolves despite more than 30 generations of wolf-free living. We focused on two modalities—the smells and sounds excreted and produced by predators.

Many species recognize the smells of their predators. We used commercially available predator urine (I kid you not, you can buy wolf pee on-line!) and placed cotton balls with a

little bit of predator or herbivore urine over a handful of food and watched how wary the marmots were when they ate the food. We found that marmots sniffed cotton balls with coyote, mountain lion or wolf urine more than elk urine. Interestingly, they did not sniff cotton balls impregnated with red fox urine, a predator on their young but not on the adults we tested. Marmots tended to look more in response to being presented coyote or mountain lion urine, and looked at similar rates when presented wolf or fox urine. Taken together, our results suggest some ability to respond to the smell of wolves. We suspect that this is because meat eaters excrete sulfurous metabolites in their urine and that the presence of other predators retains this ability to respond to these metabolites.

But what about something that differs more between predators, like their sounds? Can marmots identify wolves by their howls alone? You might say that this is silly because predators don't vocalize while hunting, but it turns out that many prey species respond to the sounds of their predators. Wouldn't you? If you were in a bad neighborhood (RMBL is a bad neighborhood for marmots!) and heard a mob of angry hoodlums wandering around, wouldn't you change your behavior and perhaps be more cautious?

In another set of experiments we broadcast coyote howls, wolf howls, and golden eagle calls to marmots eating a handful of bait. We found that marmots increased their vigilance (they looked around more) and suppressed foraging after hearing wolf and eagle calls, but didn't respond much to coyote howls. This was not due to novelty—eagle calls broadcast backwards did not elicit a response, nor did song from either a familiar non-predatory bird (white-crowned sparrows) or a novel non-predatory bird (the Australian superb fairy-wren).

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DO MARMOTS RETAIN FEAR OF EXTINCT PREDATORS?

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Wolf howls differ from coyote howls in at least two ways: wolf howls are lower frequency, and they are longer. We found some recordings of long coyote howls on the Internet and broadcast these to the marmots. Marmots responded similarly to long coyote howls and wolf howls, suggesting that howl length itself is evocative. Regardless, marmots seem to be able to respond appropriately to wolf howls.

Taken together, despite more than 30 generations of wolf-free living, marmots are able to respond to at least two cues that these predators produce—their urine and their howls. Is this ability to respond to wolves a function of convergent traits (i.e., similar sulfurous metabolites excreted by meat-eaters, and the similar howls of wolves and coyotes) or does it represent a persistence of a predator-specific adaptation? I don't know.

Based on work studying

kangaroos and wallabies in Australia I developed something I call the "multi-predator hypothesis." The multi-predator hypothesis predicts that species that still have some predators present will maintain antipredator behavioral traits even for extinct predators. This is because we should expect antipredator behavior for different predators to co-evolve. Since it wouldn't make much sense to be really good at escaping wolves and horrible at escaping coyotes and eagles, we expect animals to evolve antipredator behavior for all, and for these traits to be linked in some way. Thus, the loss of wolves wouldn't necessarily lead to the loss of wolf antipredator behavior as long as coyotes and eagles were still around.

So, despite not knowing the precise mechanism underlying the ability of marmots to respond to wolves (good research raises more questions than it answers), they seemly do so. We're doing some

experiments with life-size photographs this summer to see if and how marmots respond to the sight of wolves and other predators, but it seems that marmots will at least know that wolves are something to be feared should they re-colonize our part of Colorado.

*The author is an associate professor of ecology and evolutionary biology at the University of California Los Angeles. He spends his springs and summers in the relative safety of the Rocky Mountain Biological Laboratory, where he continues the long-term research on marmots at the RMBL started in 1962 by Ken Armitage. Read more about Dan's research by visiting his website: www.eeb.ucla.edu/Faculty/Blumstein and read more about marmots by visiting *The Marmot Burrow*: www.marmotburrow.ucla.edu.*

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