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No special permits will be issued for the purpose of irrigating newly installed landscaping, lawns and/or trees.

RMBL Notes

Nature's wake-up call: the Marmot alarm

by Daniel T. Blumstein, Ph.D.

*Editor's note: The author is an associate professor of ecology and evolutionary biology at the University of California Los Angeles. Before studying marmots at the Rocky Mountain Biological Laboratory, he spent over a decade studying seven other marmot species in Pakistan, Germany, Russia, Canada and the United States. Now 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. RoboBadger can often be spotted at the Chateau Marmont, in Los Angeles, schmoozing with movie stars.*

Second, callers could direct their calls to conspecifics—other members of their own species. Calls directed to conspecifics could have several possible functions. They could create pandemonium. Imagine you're a predator, and you're trying to focus on an elusive prey and suddenly your entire visual field erupts in running prey. Kinda hard to stay focused on your initial target, huh? Well that's the idea behind the pandemonium hypothesis: by calling, callers get other individuals to run around making it harder for the predator to kill the caller. A modification of this could be seen when animals hearing an alarm call then call in response. Wise predators would move on if the entire meadow has erupted in alarm calls.

Third, callers could direct their calls to specifically warn conspecifics. This function involves a slightly different

tent with the idea that marmots are communicating to their predators. I've not yet been able to identify the degree to which marmot alarm calls discourage attack (anybody got a trained coyote?), but by studying patterns of calling in 209 species of rodents, a student and I discovered that alarm calls initially evolved to communicate to the predators; most likely to signal that they've been detected and thus that the predators should move on. The conspecific warning functions of calling likely evolved after this initial function.

What do these calls mean? Are they like the words we use to denote objects? Or, do they simply reflect how scared an individual is when she calls? I spent a number of years studying the meaning of calls in different species of marmots (there are 14 species, found throughout the northern hemisphere). Alarm calls, because they are elicited by specific and identifiable external stimuli (e.g., a coyote, a fox, an eagle, a red-tailed hawk), could conceivably communicate specific knowledge to those animals hearing the calls.

To study meaning you want to see if there is a one-to-one mapping of predator type on call structure. Assistants and I recorded and analyzed hundreds of natural calls earned by sitting in meadows for thousands of hours and waiting for marmots to naturally call. How often do you see marmot predators? We also elicited calls by walking toward marmots, by driving a remote-controlled badger (aka RoboBadger) towards marmots, and by flying a radio-controlled glider painted to resemble a golden eagle (aka Eagle Kanivel) over marmots. Marmots don't like these model predators and they especially didn't like RoboBadger (badgers are very effective marmot predators).

If marmot alarm calls were like our words, then we would have expected a single call type to be elicited by a single type of predator. I did not find this. Rather, in all of the eight species I studied, I found that there are a remarkable diversity of ways that marmots could communicate risk. Some, like our yellow-bellied marmots, do so by varying the rate and number of calls emitted. Yellow-bellied marmots emit more calls and call at a faster pace when they're more scared. Others, like the golden marmots I studied in Pakistan, 'packaged' calls into multi-note bouts. A 12-note bout denoted a low risk, a five-note bout signaled a high risk. The critically endangered Vancouver Island marmot produces five different types of alarm calls, and the order that they emit them functions as a simple syntax. Despite this diversity of call types, they too seemingly communicate risk; their calls do not denote specific predators.

What other information is contained in marmot alarm calls? By recording and analyzing the structure of calls, I discovered that calls contain information about the age, sex, and specific identity of the caller. Moreover, by broadcasting calls back to marmots and noting how they responded, I found that marmots make use of this information.

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Did you ever find yourself hiking or riding around the backcountry wondering, why on earth are those marmots screaming at the tops of their lungs at me? The loud whistle-like chirps that our local yellow-bellied marmots emit when they are scared are referred to as alarm calls. I've spent much of a career studying the structure and function of these vocalizations. Why would someone want to study rodent squeaks? One reason is because they illustrate an evolutionary paradox.

Alarm calls, because they are so loud and easily localizable, should make it easier for a predator to locate a caller. I routinely locate marmots after hearing them call. Coyotes do the same thing. Calling is thus a risky behavior because it may increase the likelihood of a caller getting killed. The paradox is why should an individual do something risky when it could just as easily quietly retreat into its burrow. There are several possible solutions to this problem.

First, callers could be directing their calls to the predator. Most predators require stealth to successfully complete a hunt. Once they've lost this, their hunting success drops markedly. Thus, callers could essentially be telling the predator: *I see you; now you've got no chance of killing me. Go away.* Wise predators would seek a meal elsewhere.

emphasis because it involves doing something risky to help others. Darwinian logic says that such behaviors should not evolve unless the caller gets something from this. If the conspecifics warned are relatives, callers may obtain indirect fitness (i.e., by calling, they will save the genes they share with their relatives). Some species engage in complex Darwinian algebra where they vary the likelihood of calling as a function of the exact degree of relatedness to vulnerable conspecifics. Call most if you're warning your kids. Call a bit to warn nieces and nephews or cousins. Call less to warn second cousins. Don't call to warn strangers.

With all of these possible functions, what do yellow-bellied marmots do? My research has demonstrated that callers do warn relatives, but mostly it's mothers warning their vulnerable offspring. Mothers uniquely call more once their vulnerable offspring have emerged above ground. Older cousins don't increase the likelihood of calling then, nor do uncles or aunts. Calling, in yellow-bellied marmots, is primarily a form of maternal care.

But other marmots do call. And sometimes marmots keep calling long after you think they should have stopped (ever been woken up in the morning by a marmot that calls, and calls and calls?). These patterns are consis-

Nature's wake-up call

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Why would marmots be interested in the individual identity of callers? Some birds (like penguins) and mammals (like bats or seals) leave their young in a crèche (a communal day care center) while they go off to forage. Upon returning to the crèche, they must reunite with their young. There are good reasons in such systems for individuals to have distinctive vocalizations and for having the ability to differentiate individuals based solely on their vocalizations. But what about in alarm calling systems? Marmots don't alarm call that much. They're not territorial advertisement calls. Why would a marmot care who called?

We all know Nervous Nellies and Cool Hand Lucies—individuals that are afraid of everything or virtually nothing. Moreover, Nervous Nelly is probably more likely to give false alarms, by calling in response to things that may not be threatening. If marmots predictably varied in how likely they were to emit calls, then it would make sense for those who by responding would potentially interrupt a meal, to decide how to respond based on the callers' reliability.

We set out to test the hypothesis that marmots are concerned about caller reliability by artificially making a hypothetical marmot a reliable caller, and making another marmot an unreliable caller. We did this by dragging RoboBadger out of retirement. We then broadcast alarm calls from one individual immediately after a tarp over RoboBadger was removed. Marmots learned that calls from this individual were reliably associated with the presence of a nasty predator. We created an unreliable caller by broadcasting alarm calls from another individual on another occasion when RoboBadger remained covered by a tarp. We found that upon later hearing calls from the reliable individual, marmots looked up, but then quickly resumed eating (they spend a lot of time eating). Moreover, we found that when they later heard calls from the unreliable individ-

ual, they spent a lot of time independently assessing the true risk.

This was a rather unexpected discovery because we expected that the reliable callers would elicit more independent investigation and that the unreliable individual would be ignored (remember the fable about the boy who cried wolf?). What we discovered, in fact, was a very different way that reliability matters in alarm-calling systems. Thus, the marmots expanded our knowledge about the diversity of ways that alarm-calling systems could work.

How could individuals differ in their reliability? When we trap marmots they often defecate. We collect their feces and freeze them. Later, when marmots are hibernating, we extract hormonal metabolites from their feces. Glucocorticoids, like cortisol and corticosterone, are referred to as 'stress hormones' because they are emitted when animals must fight or flee an impending threat. While these hormones are likely elicited when we handle marmots, digested hormones in marmot feces reflect the physiological state long before our trapping event. We used these hormones as an indicator of the baseline levels of stress that different individuals had.

It turns out that when an individual was trapped and alarm called in the trap (they sometimes do this), they had systematically higher levels of glucocorticoid metabolites in their feces than on another occasion when they did not alarm call in the trap. Thus, systematic differences in baseline levels of stress hormones could explain why some marmots are Nervous Nellies while others are Cool Hand Lucies.

So the next time you or your dog scares a marmot and she begins to alarm call, or the next time you're throwing a snowball at a marmot who has just stolen your lunch after you've summited a high peak, I hope you'll have a greater appreciation for the diversity of animal signals and how marmots have played an important role in our understanding of the diversity of animal communication.

NOTICE OF A REQUEST FOR LETTERS OF INTEREST

The Board of Gunnison County Commissioners of Gunnison County is interested in receiving letters of interest regarding the potential to develop a partnership with a private developer in the planning and construction of essential housing to serve some of the needs of the community's work force. Gunnison County currently owns approximately 7 acres on North Colorado and approximately 1.6 acres in West Gunnison.

The Board of County Commissioners will consider mixed development where some units are not deed restricted but marketed at certain price points as well as rental units and deed restricted units.

Copies of the detailed Request for Letters of Interests (RLOI) can be obtained by contacting John DeVore, Gunnison County Manager at (970) 641-0248.

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