

mong the esoteric pleasures of the World Wide Web is a site offering a medley of chirps made by alarmed marmots around the world.

The collection now boasts alarm calls from 13 species, including a chuttering sound from America's most famous marmot, the groundhog.

To the untrained ear, these chirps and squeaks sound like, well, chirps and squeaks. A listener could easily think, "Oh, a marmot," and drift back to checking airline fares or fretting about the stock market.

But one marmot's squeak is another man's science, and marmot Web site creator Daniel T. Blumstein at Macquarie University in Sydney, Australia, is just one of a growing number of researchers who use simple squeaks to test complex ideas.

Alarm call research is booming in two major areas, Blumstein says. Researchers are exploring why animals give alarm calls at all, since making a loud noise might increase the chance of becoming some-body's lunch. Other inquiries focus on what the calls signify and what that message reveals about how animals communicate, how their brains work, and ultimately how human cognition has evolved. Not a bad job for one small chirp.

or years, people have had the notion that calling out alarms might be altruistic, but that idea was difficult to test. Altruistic behavior benefits siblings, other relatives, or the community, but at some risk, inconvenience, or cost to the performer. Tracking these benefits requires finding out who's who in a population of wild animals—and that can be a tough task.

Paul W. Sherman, now of Cornell University, broke through that barrier in 1977 with a landmark study of alarm calls in Belding's ground squirrels. Through years of monitoring—tagging ears and marking animals with hair dye— researchers had established family trees for hundreds of

ground squirrels in California's Sierra Nevada. Sherman and 10 field assistants then logged more than 3,000 hours watching the ground squirrels and their terrestrial predators. Weasels visited 67 times, badgers 11 times, and other menaces made 24 appearances.

Such observations allowed Sherman to sort through the possible benefits an animal might reap from sticking its neck up and squealing. First, he considered nonaltruistic behaviors. Did the ground squirrels' whistles themselves deter the predator? Did they incite colony members to mob the intruder, or did it create a ventriloquistic twist that misdirected an invader? Maybe the first squirrel who squealed in alarm created such pandemonium that a predator had a frenzy of scurrying targets to choose among.

Probably none of the above, at least for calls triggered by terrestrial predators, Sherman concluded. He found no mobbing, ventriloquism, or pandemonium. No predators were startled or confused by the squeals and whistles. Animals who gave the alarm whistle raised their odds of being killed, he reports.

For a different call, Sherman did find a direct benefit to the sentinel. A hawk swooping down triggers repeated whistles that send all ground squirrels racing for cover. In the chaos, the caller's chance of survival increases, so Sherman does not regard this aerial-danger call as altruistic.

Assisting relatives, however, "is the most likely function of the ground squirrels' [terrestrial predator] alarm call," Sherman says. Females, the ones who call, do so more frequently when relatives are around. If surrounded in the wild by unrelated ground squirrels, the females raise no alarms.

This result "implicates kin selection," to borrow Sherman's phrase. The idea of kin selection as an explanation for altruistic behaviors first gained ground among researchers who were studying evolution by focusing on the success or failure of genes. Because individuals have some genes in common with their relatives, favoring kin with food or protection could increase the chances that those genes would spread. Altruism toward a cousin or an aunt was not some astonishing spiritual breakthrough; it was just a way of boosting survival chances of shared genes.

The studies of ground squirrels helped broaden the kinds of benefits that researchers looked for when analyzing evolution. Instead of counting direct offspring as the only measure of the success of a beneficial trait, researchers began to look at so-called inclusive fitness, which also considers the fortunes of cousins, uncles, aunts, and hosts of other gene-sharers.

Not so fast, says Blumstein. What's true for ground squirrels may not hold for all calling animals. He has recently started arguing for a different interpretation of alarm calls. He drew his ideas from studies of another great pedigreed rodent system—the yellow-bellied marmots living in the mountains near the Rocky Mountain Biological Laboratory in Crested Butte, Colorado. Kenneth B. Armitage of the University of Kansas in Lawrence and his students have been following these animals for some 35 years.

When marmots whistle an alarm, their bodies shake, a mercy for scientists trying to figure out who's making the noise. Sometimes the marmots sound an alarm when they spot a dog or other threat, and sometimes they don't. The presence of young, vulnerable offspring nearby explains more than 40 percent of the variation in calling, Blumstein and his colleagues reported in the January 1997 ANI-MAL BEHAVIOUR. The proximity of other relatives-sisters, cousins, and so forthdid not explain more of the variation. So, Blumstein asks, why invoke the idea of inclusive fitness? "Alarm calling is a form of parental care," he concludes.

Armitage suggests that this view challenges conventional kin selection theory. He evokes the late J.B.S. Haldane's image

of kin selection as somebody sacrificing his life for two brothers or eight cousins. Instead, in marmots, Armitage argues, "they don't cooperate at all with distant kin. Cousins become competitors."

Yes. says Armitage, he is perfectly aware of the extensive models that ground the theories of kin selection, and he finds the math impressive. The problem is the marmots. "They don't know these mathematical models, I guess," he says.

How the alarm-call debate will sort out is not clear. Armitage and Blumstein have prepared a commentary on the problem for an upcoming issue of Animal Behaviour. Sherman and a colleague have written a counter-commentary for the same issue, which inspired a counter-counter-commentary. "We're having a shoot-out," Blumstein says cheerfully.

Sherman clarifies that the articles are "an exchange of views from slightly different perspectives." As he sums up his group's paper, "the nub of our disagreement is that we believe that parental care is very much a part of kin selection."

lumstein and Armitage have also looked at marmot data for clues to what the calls might mean. The animals seem able to communicate approximate degrees of risk, the researchers reported in the January 1997 ANIMAL BEHAVIOUR.

The scientists watched how marmots responded to both natural invaders and to such test nuisances as trained dogs, a model badger, a radio-controlled glider, and, of course, a researcher trudging toward the colony. There was no evidence that marmot calls are unique to any group of threats, the researchers report. Yet, the marmots whistled faster as dangers got closer. Playing back the calls confirmed that the rapid vocalizations inspired extra alarm in the rest of the colony.

Yellow-bellied marmot noises seem rather tame compared to the vervet monkey repertoire that ignited the search for content in alarm calls. When a monkey on the ground detects a large carnivore like a leopard nearby, it gives a "wrrs" call, and the other monkeys scramble up trees, Tom Struhsaker of Duke University in Durham, N.C., reported in 1967. But if

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an eagle swoops by, the alarm call becomes a grunt, and animals dive into underbrush to hide. A snake provokes chuttering sounds, causing monkeys to stand up on two feet and peer at the ground around them.

Were the calls themselves conveying the nature of the menace, or were listeners somehow picking up other clues from the context? To find out, Robert M. Seyfarth and Dorothy L. Cheney, now of the University of Pennsylvania in Philadelphia, and Peter R. Marler of the University of California, Davis played recordings of the calls, with no caller or predator present to provide hints. The monkeys responded appropriately in the three different ways.

One interpretation might be that the vervet monkeys are doing the same thing the marmots are doing—merely communicating their degree of alarm. That does not seem likely to Marc D. Hauser of Harvard University, who revisits the classic experiment in his book *The Evolution of Communication* (1997, MIT). The playback experiments included variations on each type of call, such as short, faint "wrrs" as well as long, loud ones. Yet, these qualities, possible indicators of how alarmed the calling animal is, do not seem to affect the other animals' reactions, he points out.

More recent work on vervet monkeys has explored how the little ones get the hang of such an elaborate system. For the first 2 or 3 years, they don't do too well, raising a ruckus about harmless sights, report Hauser, Cheney, and Seyfarth.

However, even during this befuddled period, young vervet monkeys restrict their eagle alarm calls for things in the air, even if they are just falling leaves. The researchers have also heard snake alarm calls for innocuous ground-related phenomena, such as branches crashing down through a bush. The monkeys may use a basic, inborn category, such as scary things in the air, he says. "What is unclear, however, is how experience fine-tunes this category."

The confusion displayed by young vervets might just be errors typical of growing up, but Hauser also raises the possibility that youngsters may be using



Chicken alarm calls are no random squalks. When something threatening approaches on the ground, a chicken sounds an alarm. When a laboratory chicken hears a recording of the call, it stands tall and scans the landscape (left). However, recordings of calls triggered by a hawk swooping from the sky prompt a chicken to crouch and check for aerial troubles (right).

the alarm calls as a way to question whether that crashing thing, or that flying thing, is worth worrying about. Observations show that young vervets who raise an appropriate alarm, triggering much calling and dashing about among adults, are more likely to produce the correct alarm the next time than are those who call inappropriately, he reports.

Specific alarm calls may not be much of a surprise in a primate, but what about animals farther removed from the humans, with their communication prowess? "Surely, the humble domestic chicken would fall close to the bottom of the mental heap," Hauser notes. Yet, Chris Evans of Macquarie University has spent much of the last 10 years trying to figure out what chickens are squawking about.

As Hauser sees it, if chickens also give different kinds of alarm calls, "then either the psychological mechanisms underlying this communicative skill are less sophisticated than originally claimed or chickens have the same sorts of cognitive abilities as do vervets."

Indeed, domestic chickens and jungle fowl, their wild relatives, give different alarms depending on whether the approaching menace comes from the air, like a hawk, or from the ground, like a raccoon. Video technology allows the researchers to test reactions to various intruders, even an image of a raccoon flying through the air.

Playing back the resulting collection of alarm calls to laboratory chickens confirmed that the animals respond differently to the call for danger from above than to that for danger from the ground.

Tests of other animals' alarm calls have produced mixed results. Ring-tailed lemurs have both aerial and terrestrial alarms, but ruffed lemurs do not. Ground squirrels do not seem to communicate such a difference, but Gunnison's prairie dogs might.

All in all, studies of alarm calls may be inching closer to a conclusion that some animals convey specific information in their calls—a feat once thought to be uniquely human.

Stepping back from the debate, Hauser admonishes his fellow humans to play fair with the evidence. "Let's face it. We have, and probably always will have, an obsession about our uniqueness," he observes.

Whenever animals are found to demonstrate humanlike cognitive processes, people's blood pressures rise. "Every time a discovery has been made that challenges our domination of the animal kingdom, we are disbelieving at first and, once convinced, unleash all of our intellectual horsepower and search for something else that will set us apart from them," Hauser notes.

So are chickens really yelling "incoming aerial danger"? And are monkeys refining their sense of what's worth wrrs-ing about? Maybe it's our turn for an EEEEK.