Feeling the heat: Ground squirrels heat their tails to discourage rattlesnake attack

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Predators have a remarkable evolutionary effect on the morphology and behavior of their prey (1). In their attempt to reduce the likelihood of being killed, prey species have evolved a variety of counterstrategies, including the ability to communicate directly with their predators to discourage pursuit or attack. Stotting, when ungulates jump up in a stereotypical stiff-legged display, is a visual signal of unprofitability to hunting carnivores, and the alarm calls and mobbing behavior seen in birds and mammals may also discourage pursuit. Indeed, predators are hypothesized to be the ancestral target of alarm communication in rodents (2), systems that ultimately have been exapted to serve sophisticated conspecific warning functions (3). Communication requires a signaler to influence the behavior of a receiver by using one or more modalities. Previous studies have focused on visual, acoustic, seismic, and olfactory modalities, but in this issue of PNAS, Rundus *et al.* (4) have discovered that California ground squirrels (*Spermophilus beecheyi*) communicate by means of a private infrared channel specifically to a major predator that is uniquely sensitive to infrared radiation—rattlesnakes (*Crotalus oreganus*)—whereas encounters with infrared-insensitive gopher snakes (*Pituophis melanoleucus*) elicit snake-directed tail flagging without the infrared signal.

Squirrel–Snake Dynamics

Life is tough if you are a ground squirrel; you and your offspring fall prey to a variety of raptors, carnivorous mammals, and snakes. We would expect such prey to have evolved a sophisticated set of antipredator behavior, and, indeed, studies of sciurid rodents have identified a complex set of individual and cooperative strategies to avoid predation.

Snake-elicited antipredator behavior has been particularly well studied in California ground squirrels. Adult ground squirrels living sympatrically with poisonous rattlesnakes have proteins that bind to the venom and provide immunity to rattlesnake bites (5). Rattlesnakes search for and explore squirrel burrows to find squirrel pups, which, not having developed the proteins, are vulnerable to rattlesnake predation. Squirrels aggressively protect their pups from poisonous and nonpoisonous snakes by mobbing them (6).

California ground squirrels are exquisitely adapted to confronting rattlesnakes. They are able to assess the relative risk of rattlesnakes by listening to their rattles (7, 8). Large snakes produce lower-frequency rattles, and warm and potentially dangerous snakes rattle faster than cold snakes. Squirrels will approach a colder and therefore slower snake more closely than a warmer and more dangerous snake. Squirrels signal their presence and harass snakes by kicking dirt and pebbles in their faces (9). They piloerect and flag their tails from side to side to either intimidate their rival or potentially make a large, moving (but benign) target for the snakes to attack. Interestingly, and unlike their response to other predators, squirrels are less likely to emit alarm calls when they encounter snakes (10); but, then again, snakes would not hear such alarm calls. Snake harassment exploits the sensory modalities to which snakes are most attuned: tactile and visual. Importantly, snake harassment by squirrels seems to be successful: snakes respond defensively (11) and may move away after the squirrel's harassment.

Multimodal Communication

Students of animal communication have traditionally studied a single modality at a time, but recently, there has been interest in looking at how the modalities work together (12, 13). Such multimodal communication can work in various ways. Because all signals degrade between the time they are produced and the time they are perceived, each modality could provide a redundant signal and, by doing so, ensure that a single message gets across. Alternatively, the intensity of a response to constituent signals could be greater than to a single signal and thus illustrate enhancement. Multimodal signals could also be nonredundant, where each constituent signal provides different information. In this case, the sum of different constituent signals could lead to different responses, or one modality/signal could dominate the other. The combination of different modalities could modulate the response, or, theoretically, a novel response could emerge. The challenge when studying multimodal communication is to identify salient modalities and then experimentally study them.

Recent advances in video analysis and playback techniques have enabled researchers to quantify and study the meaning and efficacy of visual signals with unprecedented control (14), and this has begun to generate novel findings about multimodal communication (15). Although many animals respond to video images, some researchers have elected to capitalize on recent technological advances in robotics to develop realistic models that can be deployed to study multimodal communication (16).

Wise prey should "speak the same language" as their predators if they hope to discourage attack. In a compelling set of observations and experiments, Rundus *et al.* (4) focused on an entirely novel modality—thermal emissions produced by squirrels—and demonstrated that squirrels directly target these infrared signals to rattlesnakes. Rattlesnakes have a pit organ that enables them to find warm-blooded prey by detecting infrared emissions. Thus, rattlesnakes, among all other squirrel predators, are uniquely sensitive to these thermal signals. Using a thermal-imaging device, Rundus *et al.* discovered that squirrels only heat their tail when encountering rattlesnakes. This heat was not the byproduct of increased physical activity but rather the result of specifically warming their tail. Then, using a robotic squirrel that could both flag and heat its tail, Rundus *et al.* found that the response by rattlesnakes was enhanced when both potential signals were deployed. Rattlesnakes became more cautious when a squirrel flagged its heated tail. Rundus *et al.* speculated that the heat increases the apparent size of the squirrel. Because squirrels aggressively attack and may bite a snake, and larger squirrels are more threatening to snakes, inducing caution in snakes should be an effective defense by the squirrel.

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Thus, the squirrels have a multimodal composite signal that enhances their ability to discourage attack by snakes. By contrast, although the full repertoire of other snake-harassment techniques is deployed when squirrels encounter gopher snakes, squirrels do not warm their tails because gopher snakes do not have pit organs and thus are not thermally sensitive. California ground squirrels have evolved a specific thermal defense to a species that specializes in thermal receptivity.

Baron von Uexküll (17) emphasized that to understand non-human behavior, we must understand the *umwelt*, or perceptual world, of animals. Some models of communication and sexual selection formally recognize the importance of producing signals in modalities, and in ways, to which receivers are sensitive (18, 19). What is so interesting about the study of Rundus *et al.* (4) is that they have discovered a heretofore hidden channel in communication that apparently is not used by the squirrels when communicating with each other but rather evolved specifically in response to a modality that is unique to a specific dangerous predator.

Rattlesnakes became more cautious when a squirrel flagged its heated tail.

Antipredator behavior is a potent evolutionary force that can lead to novel adaptations. Most prey are threatened by more than one predator, and the evolutionary dynamics of responding to multiple predators are an area of much interest (20, 21). The work of Rundus *et al.* (4) should encourage us to look more broadly for mechanisms by which animals assess and manage predation risk to each of their predators because each predator may require a slightly different strategy to be evaded or manipulated. In addition, we should not forget von Uexküll's lesson to view animals from their, and not our, perceptual world.

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