3 The Cognitive Defender: How Ground Squirrels Assess Their Predators

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Ground squirrel 09 flagged her fluffed-out tail from side to side as she explored the area around a burrow where we had last seen a rattlesnake. Followed by five of her pups, she then traveled to a burrow where her adult son from a previous year was living. Squirrel 09 left her youngsters there as she began traveling to and fro several times, alternately looking for the snake at the original location and returning to interact with her babies. On some of these excursions, she was accompanied closely by one or more of her pups, who often followed in a tight little "flock." Finally, 09 spotted the snake and approached it very closely, flagging her tail, jumping back, and reapproaching repeatedly. One pup had followed her to the snake, and as the mother continued to deal with the snake, two more pups joined them, and later a fourth. Our concern for the young squirrels intensified as they also began to confront the snake, behaving much as their mother did. Surprisingly, 09 did not step forward to protect her babies when one of them approached the snake. However, she was most consistently the closest squirrel to the snake, and her presence there appeared to keep the pups out of this dangerously close region.

As the snake continued its exploration of the area, 09 led four of her pups back to her son's burrow and all five squirrels went underground there. A little later, a fifth youngster arrived at the same burrow, wobbly, limping, and not using its left forepaw, apparently snake bitten. We never saw this pup again after its mother emerged to lead it into the burrow. Subsequently, 09 reemerged and resumed her search for the snake, which was no longer in view. During this time, some of her pups intermittently accompanied her, perhaps endangering themselves again. After more than an hour of dealing with this snake, mother and pups could no longer locate it. They gradually calmed down and began to feed in preparation for the coming night. But their problems were not over. The snake harassed this family for three more days, killing a second pup, and blind-siding 09 by delivering a sublethal bite to the side of her face where she had earlier lost her sight.

Exploring What Ground Squirrels Know about Their Predators and How They Know It

My research program has long focused on predatory contexts like this one in order to explore the behavioral abilities of California ground squirrels (*Spermophilus beecheyi*). This rattlesnake episode illustrates the challenges that ground squirrels face in dealing with the problems they encounter in nature. Here the maternal ground squirrel had to juggle at least three different tasks, i.e., keeping herself safe while also protecting her pups and managing the behavior of the rattlesnake. The best way for squirrels to proceed in such situations depends on the details of the threat they face, and they must apply their cognitive systems to the task of uncovering those details and finding a way to proceed, as we will see later. The use of predatory contexts ensures that I am studying behavior in situations that are meaningful to my animals in an evolutionary and ecological sense. In this way, I maximize my chances of discovering behavioral processes that have been most strongly shaped by natural selection and individual experience during development. Toward that goal, I have studied the antipredator activities of ground squirrels as they deal with the variety of predators that have historically been important to them, including not only rattlesnakes but also gopher snakes, badgers, coyotes, bobcats, red-tailed hawks, and golden eagles.

These different classes of predators use different hunting techniques that require different antipredator strategies. Avian predators pose the most immediate threat to squirrels, appearing suddenly and launching rapid aerial attacks. More slowly moving mammalian predators pose threats of intermediate urgency; and very slowly moving, ambush-hunting snakes pose the least immediate threat. Ground squirrels vary their antipredator response to these different threats in ways that reflect a tradeoff between self-preservation and the acquisition of additional information about the predators (Coss and Owings 1985; Owings and Hennessy 1984).

Activities that facilitate assessment require getting close to and maintaining sensory contact with the predator, which increases the squirrel's vulnerability to the predator. Activities that reduce a squirrel's vulnerability, for example by minimizing conspicuousness, often involve staying farther away from the predator, which reduces access to assessment cues. Where danger is most immediate, as with avian predators, squirrels opt for more self-preservation by evading the predator and maintaining a low profile. As a result, their options for assessment are limited. In contrast, where the danger is least immediate, as with snakes, squirrels are able to emphasize assessment more heavily by approaching and interacting with the snake as squirrel 09 did.

Thus squirrels shift the balance among the conflicting demands of assessment and self-preservation in ways that indicate that they know how the immediacy of threat from their various predators differs. The demonstration of such knowledge is the first important step in the biological study of cognitive processes (Kamil 1994).

The next step is to explore *how* these animals know what they know. Our research on this type of question has concentrated on the relationship between ground squirrels and snakes. Throughout much of their range, California ground squirrels are the prey of both Pacific gopher snakes (*Pituophis melanoleucus catenifer*) and northern Pacific rattlesnakes (*Crotalus viridis oreganus*). Venomous rattlesnakes are more dangerous than nonvenomous gopher snakes, a difference indicated by the fact that these squirrels comprise 69 percent of the diet of rattlesnakes, but only 44 percent of the diet of gopher snakes in the foothills of the central Sierra Nevada of California (Fitch 1948, 1949). Nevertheless, the danger posed by rattlesnakes is moderated by blood proteins that confer resistance to rattlesnake venom in both young and adult California ground squirrels (Biardi et al. 2000; Poran and Coss 1990). Despite this resistance, pups succumb to rattlesnake bites because they cannot neutralize as much venom as adults can. Consequently, rattlesnakes almost exclusively eat pups, and adult squirrels can be quite assertive in defending their pups, risking injury but not death from a rattlesnake bite (Fitch 1949; Poran and Coss 1990).

These squirrel–snake relationships comprise a very useful set of predator–prey systems for studying processes of predator recognition and assessment, for at least two reasons. First, squirrels have had a long time to evolve such cognitive defenses against these snakes; according to the fossil record, the ancestors of modern rattlesnakes and gopher snakes have been potential sources of natural selection in ancestors of California ground squirrels for as long as 10 million years (Coss 1991). Second, squirrel–snake encounters lasting hours or even days (as for squirrel 09) provide abundant time for recognition and assessment of snakes.

Our research on snake recognition and assessment has explored both the details and the development of these processes. We have discovered that California ground squirrels do not require experience with snakes during development in order to recognize them. Pups of just postweaning age, born and reared in the lab without contact with snakes, have impressed us with their sophistication. They distinguish snakes from novel animate objects when tested alone and behave in the complex ways adults do toward snakes, flagging their tails, approaching cautiously, investigating in elongate postures, throwing substrate, and jumping back (Owings and Coss 1977). Apparently pups use both visual and olfactory cues to recognize snakes. Preweanling pups, 40 to 41 days old, become alarmed by the odor of gopher snakes and will cautiously investigate a ruler painted on the wall of the test chamber, a visual pattern resembling a gopher snake or rattlesnake with transverse patterning.

However, these findings do not mean that experience with snakes is unimportant in the development of cognitive antisnake defenses. More subtle aspects of antisnake cognition may require the refinements of learning. For example, some (but not all) populations of California ground squirrels appear to require experience with snakes in order to develop the ability to distinguish rattlesnakes from gopher snakes (Coss et al. 1993). The development of such subtle distinctions may depend in part upon becoming attuned to the defensive sounds that the snakes produce in response to confrontive squirrels. Rattlesnakes rattle when pressed by squirrels, and experimental elimination of the rattling sound leads to attenuation of the antisnake behavior of adult squirrels (Rowe and Owings 1978). Closely related populations of California ground squirrels that differ in their current contact with rattlesnakes also differ in their perception of danger from playbacks of rattling and other sibilant sounds (Rowe et al. 1986), a contrast that may be generated by greater rattlesnake experience in one population than the other.

California ground squirrels are also sensitive to variation in the danger posed by rattlesnakes. For example, large rattlesnakes pose a greater threat than small rattlesnakes because larger rattlesnakes deliver more venom per strike (Kardong 1986) and strike with higher velocity and over longer distances (Rowe and Owings 1990). (Unlike birds and mammals, rattlesnakes grow throughout their lives, so that adult sizes are more variable within species of rattlesnake than within species of birds or mammals.) California ground squirrels differentiate large from small rattlesnakes in ways that are similar to their discrimination of snake species; they stay farther back from larger rattlers, but monitor them and signal more persistently (Swaisgood et al. 1999a). Body temperature also influences the danger that a rattlesnake poses; rattlesnakes are ectotherms, so that their body temperature varies more than that of endothermic birds and mammals. As a snake heats up, the biochemical processes that support behavior speed up, with the consequence that warmer snakes are more dangerous because they deliver strikes with higher velocity, less hesitance, and greater accuracy (Rowe and Owings 1990).

Thus squirrels need to know about a rattlesnake's size and temperature, but extracting this information is not as straightforward as it might initially seem. Squirrels might assess body size visually, but they often encounter snakes in the darkness of burrows or thick vegetation where visual cues about rattlesnake size are limited (Coss and Owings 1978). The detection and assessment of rattlesnakes is difficult even in well-lighted, open locations because rattlesnakes are so cryptic (Hennessy and Owings 1988; Hersek and Owings 1993). The assessment of snake body temperature can represent an even greater challenge. Simple thermal cues such as ambient temperature can be unreliable predictors of a rattlesnake's body temperature, which can change rapidly as a function of microclimatic conditions (Gannon and Secoy 1985). An assessment of snake size and temperature is further complicated by the possibility that small and cold snakes would benefit from hiding their vulnerability because they are susceptible to attack by aggressive adult squirrels.

The squirrels' solution to this assessment challenge is proactive in two ways; they use very interactive methods to gain access to size and temperature cues, and the cues they use are by-products, not formalized features of the snakes' defensive signaling. By confronting rattlesnakes, squirrels place snakes on the defensive and induce them to rattle, a sound that leaks clues about both size and temperature. Larger rattlesnakes rattle with higher amplitude and lower dominant frequencies, cues that are available as a by-product of the larger tail-shaker muscles of bigger snakes and the lower resonant frequency of their larger rattles. Warmer snakes rattle with faster click rates, higher amplitudes, and shorter latencies, all features that are by-products of the fact that higher temperatures speed snakes up. In field playback studies, these ground squirrels demonstrated their ability to use both categories of acoustic cues by responding with greater caution to the sounds of larger and warmer snakes (Swaisgood et al. 1999b).

Conceptual Framework, Implications, and Future Directions

The term *cognition* refers most fundamentally to all of those processes by which organisms come to know about their environments. The acquisition of this knowledge (knowing) can take a lot of forms and involve a lot of body parts. Ground squirrels, for example, use more than their sense organs and brains to obtain information about rattlesnakes; they also integrate their forelegs and the rattlesnakes' rattles into a "knowing loop," throwing substrate to elicit the rattling so useful for determining the species, size, and temperature of the snake they are dealing with. From this perspective, cognitive processes are embodied processes, but they are not internal to the organism like brain processes are; they are emergent properties of whole organisms (Fragaszy and Visalberghi 1996; Mason 1986; Michaels and Carello 1981). Such a view of cognition helps us to shed our anthropocentric views of how animals acquire knowledge, and instead to think of cognitive processes as fundamental to all organisms, not as a small set of special abilities confined to "a handful of privileged evolutionary newcomers" (Mason 1986, p. 306).

The processes of acquiring knowledge serve and are guided by equally broadly distributed processes of wanting (Mason 1986; Owings 1994). Wanting refers to psychological processes that involve both motivation and emotion, i.e., processes involving action based on an evaluation of objects and events (e.g., how important a snake is and therefore how much attention, time, and energy should be dedicated to dealing with it). As Mason has noted (1979, p. 225): "From a biological perspective the two great themes in the evolution of behavior are 'wanting' and 'knowing.' ... And surely it will be apparent that these themes are interwoven throughout evolution. Knowledge, for the vast majority of organisms, is pragmatic and utilitarian: Animals are prepared to know what they need to know." It follows that most of an organism's cognitive activities involve "hot" judgments about the personal significance of events, rather than "cold" assessments about how things work in general.

The interrelatedness of wanting and knowing is very evident in the antisnake behavior of California ground squirrels. For example, we have already seen how these squirrels make accurate judgments about the danger posed by rattlesnakes, e.g., staying farther back from larger snakes and monitoring them more consistently. Such assessments are, however, very much dependent on the significance of rattlesnakes to the individual squirrel. In particular, rattlesnakes are more important to maternal females with vulnerable pups than to any other class of adult squirrels. Thus mothers with young pups spend more time dealing with rattlesnakes than do nonmaternal adult females or adult males (Swaisgood et al. 1999a). Mothers are also more discriminating, distinguishing much more clearly both among rattlesnakes of different sizes and among the rattling sounds of snakes of differing temperatures and sizes (Swaisgood 1994). Similarly, all squirrels are sensitive to where they discover a rattlesnake; when a snake is found near their own burrow, squirrels are more confrontational and engage in much more tail flagging than when they detect a snake near someone else's burrow (Swaisgood et al. 1999a).

Like most research, this program has raised as many questions as it has answered. We have not explored the many distinct processes that fall under the heading of wanting as discussed, for example, by Berridge (1996). Similarly, the broad definition of cognition offered here does not imply that all animals function at the same level of cognitive complexity (for discussions of levels of cognition, see Capitanio and Mason 2000; Dennett 1983).

We have some intriguing hints of complexity in this antipredator system. For example, these squirrels behave as though they know (1) *where* their danger from snakes is greatest [e.g., in burrows and other areas where visibility is poor (Coss and Owings 1985; Hersek and Owings 1993)], (2) *how long* snake danger persists [days, because snakes lie in ambush that long (Hersek and Owings 1993)], and (3) *how to* lead rattlesnakes away from the burrows housing their pups (Hennessy and Owings 1988). Future research could explore the levels at which these squirrels function cognitively, focusing especially on how specialized these cognitive mechanisms are for the antisnake context that has been such a strong source of natural selection in this species (see Cheney and Seyfarth 1990 on the domain specificity of cognition). Variation among populations will be especially valuable in such research. Not all populations of these squirrels have consistently been under selection from rattlesnakes or gopher snakes in their recent evolutionary history, and relaxation of selection from snakes is associated with reductions in resistance to rattlesnake venom and changes in the higher-level organization of antisnake behavior (Coss 1999).

Some of the most fascinating future research will explore developmental questions. As we have already indicated, many features of this remarkably complex behavioral system develop without experience with snakes. Such findings beg for detailed studies of cognitive mechanisms, including how these mechanisms change during development and what kinds of inputs are important in their ontogenetic modification. We know that the higher-level organization of antisnake behavior is altered as squirrels mature; pups and adults, for example, use the tail-flagging signal differently. However, these differences do not simply reflect the incompleteness of development in young squirrels. Pups tail flag differently but not less proficiently; they are more skillful than adults in using tail flagging to keep other squirrels near, and they tail flag in ways that distinguish more clearly than adults do between snake-free days and days when snakes have been seen at the site (Hersek and Owings 1994).

Such findings are not unique to the development of tail flagging (Owings 1994; Owings and Loughry 1985). Young animals in general are more than incompletely developed adults; different ages occupy distinct developmental niches, with associated adaptive differences in behavior (for elaboration of this idea, see Galef 1981). Such observations raise very exciting questions. How are corresponding cognitive systems transformed as young animals mature? Do cognitive systems undergo metamorphosis in ways analogous to the metamorphoses that transform caterpillars into butterflies? If so, how do animals navigate the uncertain terrain that lies between stable stages of cognitive functioning? The study of cognitive development from this perspective of "ontogenetic adaptation" (Alberts 1987) is one of the greatest challenges in the biological study of cognition.

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