

# The Rattling Sound of Rattlesnakes (*Crotalus viridis*) as a Communicative Resource for Ground Squirrels (*Spermophilus beecheyi*) and Burrowing Owls (*Athene cunicularia*)

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Animal communication involves very dynamic processes that can generate new uses and functions for established communicative activities. In this article, the authors describe how an aposematic signal, the rattling sound of rattlesnakes (*Crotalus viridis*), has been exploited by 2 ecological associates of rattlesnakes: (a) California ground squirrels (*Spermophilus beecheyi*) use incidental acoustic cues in rattling sounds to assess the danger posed by the rattling snake, and (b) burrowing owls (*Athene cunicularia*) defend themselves against mammalian predators by mimicking the sound of rattling. The remarkable similarity between the burrowing owl's defensive hiss and the rattlesnake's rattling reflects both exaptation and adaptation. Such exploitation of the rattling sound has favored alternations in both the structure and the deployment of rattling by rattlesnakes.

Von Uexküll (1934/1957), in his classic book on the *Umwelt*, or self-world of animals, described the functional cycles that link organisms to their environments. The concept of the functional cycle illustrated how the *Umwelt* was founded on much more than just an organism's perceptual abilities; it also depended on the repertoire of effector activities that an organism has available to operate on its environment. The concept of functional cycle was a precursor of an assessment–management approach (A-M) to communication (Hennessy, Owings, Rowe, Coss, & Leger, 1981; Owings & Hennessy, 1984; Owings & Morton, 1998). According to A-M, communicative behavior reflects underlying regulatory processes in which signaling animals are reciprocally connected to

the targets of their signals by way of feedback loops, completing a regulatory circuit much like Von Uexküll's functional cycle. In Von Uexküll's *Umwelt*, there are two facets of organismic action: receptor signs and effector signs. This distinction, when combined with the concept of the functional cycle, parallels the distinction between assessment and management that has been identified for the two facets of communicative action (Hennessy et al., 1981; Owings & Morton, 1998).

The regulatory analogy that underlies A-M highlights the point that communication is a process, not a series of signal–response events (Owings & Hennessy, 1984). The interindividual process of communication is driven by the two self-interested, equally important individual activities of assessment and management. Assessment refers to the aspect of communication that is often called *mind reading*, *perceiving*, or *receiving*, whereas management has to do with that facet of communication that is often called *manipulation*, *signaling*, or *sending*. Assessment involves the quest for the affordances (Gibson, 1979/1986) that organisms need to pursue their own ends. Management is synonymous with regulation; organisms pursue their own regulatory ends in part by regulating or managing the behavior of others. Of these two individual processes, the one that has traditionally been emphasized in the study of animal communication is management, the individual process that includes emitting signals (Owings & Morton, 1997). However, the individual process of assessment has been gaining visibility in the literature and is now approaching parity with management. Management and its associated signals are now recognized as working and even originating through the process of capitalizing on assessment systems. Communication rests firmly on the foundation of both of these processes and is driven by the interplay between them (for a review, see Owings & Morton, 1998).

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Our goal in this article is to describe how a particular signal of relevance to many organisms, the aposematic warning rattle of rattlesnakes, has been exploited by the assessment and management systems of other species. In particular, we describe how California ground squirrels (*Spermophilus beecheyi*), in assessing the danger posed by rattlesnakes (*Crotalus viridis*), have uncovered very useful assessment cues in the rattling sound that are by-products of physical and physiological constraints. We also describe how burrowing owls (*Athene cunicularia*) have incorporated a rattlelike sound into their managerial repertoire, defending themselves from mammalian predators by mimicking the sound of rattlesnakes. Finally, we illustrate the exaptive and adaptive processes involved in signal evolution by presenting evidence that the burrowing owl mimetic hiss was derived from a food-begging vocalization, and we describe the changes involved in the evolution of the mimetic hiss.

### Rattling by Rattlesnakes: An Aposematic Signal

Rattling functions as an aposematic signal, that is, as a signal to potential predators of rattlesnakes that these snakes are venomous (see Discussion). Prey species signal aposematically to predators to advertise a variety of noxious qualities, for example, Monarch butterflies (*Danaus plexippus*) signal their toxic chemicals, wasps signal their painful stings, skunks signal their irritating sprays, and venomous snakes signal their debilitating bites (see reviews in Edmunds, 1974; Wickler, 1968). Aposematic signals typically consist of conspicuous colors (Cott, 1940), odors (Eisner & Grant, 1981), sounds (Dunning, Acharya, Merriman, & Ferro, 1992), or behavior patterns (Lariviere & Messier, 1996). Like agonistic signals, aposematic signals are favored because they resolve encounters without the risk of injury to either prey or predator that could result from a predatory attack, even if the attack is successfully repelled. Nonetheless, such a mutually useful outcome is possible only if the predator associates the aposeme's signal with its noxiousness. Thus, the potential predator plays a strong role in the evolution of an aposematic signal both because it is selected to avoid encounters with the potential prey's noxious qualities and because the signal must work through the predator's assessment system.

Although predator avoidance of aposematic prey may be expressed on the first encounter with the aposeme (e.g., Smith, 1975), many empirical (e.g., Brower, 1969) and theoretical (Huheey, 1988; Speed, 2000) investigations suggest that learning often plays a significant role in predators' development of aversions to aposemes. In A-M terms, this means that the aposeme often must establish or augment the assessment rule of thumb about what cues are associated with danger before that assessment rule can be exploited. Warning signals that stand out dramatically from the background might enhance the predator training that results from pairing these signals with the aposeme's noxious qualities. Several experiments have indeed demonstrated that naive predators learn to avoid conspicuously colored noxious prey more easily than cryptically colored noxious prey (Gittleman & Harvey, 1980; Gittleman, Harvey, & Greenwood, 1980; Roper & Wistow, 1986; Terrick, Mumme, & Burghardt, 1995). Moreover, bright, conspicuous colors may also reduce the chance that an already trained predator may mistakenly attack unpalatable prey during the heat of

an encounter (Guilford, 1986) or that a predator may forget the association between the aposeme and its signal (Speed, 2000).

Identification of the benefits that might maintain aposematic signals has proven to be easier than explaining how such signals might originate. The paradox, long recognized by biologists (Brower, 1984), is that the first brightly colored individual in a population of noxious but cryptically colored prey would only draw additional attention from predators. If such predators must learn to associate the prey's noxiousness with its conspicuousness, the prey may not live through the training. How then can aposematic signals arise? One possibility is through kin selection, an idea initially suggested by Fisher (1930). However, individual selection has also proven to be a possibility (Malcolm, 1990; Sillén-Tullberg, 1988), especially when prey are protected by tough exoskeletons (Wiklund & Järvi, 1982), thick shells (Rosenberg, 1989), or debilitating venom and can therefore withstand the initial attacks of an untrained predator.

The most commonly described aposematic signals are visual (see reviews in Brower, 1988; Cott, 1940; Wickler, 1968), but this may reflect the perceptual biases of humans more than the relative frequency of visual aposematic signals (Pough, 1988). Some animals are known to deploy acoustic aposematic signals, the best known of which is the rattling sound of New World pit vipers called rattlesnakes. Their buzzing, hisslike noise (see Figure 1) is produced by a loosely interlocked string of highly modified scales (Klauber, 1972; Zimmermann & Pope, 1948) shaken by tail muscles that appear specialized for rattling (see review in Moon, 2001). The evolution of the rattlesnake rattle does not pose the same difficulties as described for visual signals that are continuously on because an occasionally deployed rattling sound does not compromise the snake's ability to be cryptic. Nevertheless, accounting for the evolutionary origin of rattling has engendered

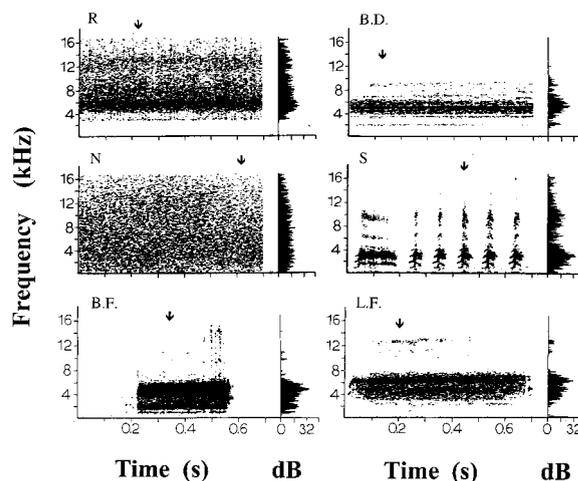


Figure 1. Frequency by time and frequency by amplitude (dB) spectrograms of six sounds. Frequency by amplitude was sampled from the point in each sound indicated by the arrow. R = representative portion of the rattling of a large (850 g) rattlesnake; B.D. = representative portion of a vocal defensive hiss from a burrowing owl; N = representative portion of white noise; S = complete scream chatter from a burrowing owl; B.F. = complete food-begging hiss of a burrowing owl; L.F. = complete food-begging hiss of a little owl.

considerable scientific debate (see reviews in Greene, 1988; Klauber, 1972; Moon, 2001; M. P. Rowe, Farrell, & May, in press; Schuett, Clark, & Kraus, 1984). A growing consensus suggests that rattling evolved from the defensive tail vibrations that are characteristic of numerous species of both poisonous and harmless snakes (Greene, 1988), behavior that may have originally functioned to divert an enemy's attention away from the snake's more vulnerable head and toward its more expendable tail (Garman, 1889; Greene, 1973; Williams, 1966). Tail vibration may have subsequently acquired a warning function in dangerous species such as rattlesnakes. Protorattles could then have been selected because the startling sound, just like bright colors, might make it easier for enemies of rattlesnakes to learn and remember the snake's dangerousness. That the rattle currently functions as an aposematic display of this danger is not disputed, as all 29 extant species of rattlesnake currently use rattling only when threatened (Greene, 1988; Klauber, 1972).

Surprisingly few data are available on how potential predators of rattlesnakes respond to the rattling sound (but see Klauber, 1972). The best data have to do with members of a prey, such as California ground squirrels, rather than predator species. These ground squirrels evoke rattling by approaching, throwing substrate at, and closely investigating the snake in elongated postures (M. P. Rowe & Owings, 1978). Such contact-promoting activities by the squirrel quickly subside when the snake rattles and are replaced by contact-reducing activities such as startling, freezing, and running away. This short-term "backing-off" effect of rattling contrasts with the long-term effect evident in the same study. In this experiment, California ground squirrels were allowed to interact on separate trials with rattlesnakes whose rattles were either silenced or audible. The squirrels engaged in more vigorous and prolonged confrontation with the rattlesnakes when the rattling sound was audible, a finding that suggests that rattling can be a two-edged sword.

In fact, the defensive behavior of rattlesnakes appears to reflect the snakes' sensitivity to the costs that accompany the benefits of rattling. Rattlesnakes deploy defensive behavior in a very context-sensitive way. The first reactions of rattlesnakes to potential danger are either to remain cryptic or to attempt escape. If neither tactic averts danger, these snakes often become defensive, threatening with a ready-to-strike posture, and typically start rattling (Duvall, King, & Gutzwiller, 1985; Greene, 1988). However, the latency to begin rattling depends on contextual details related to the risk the snake faces. Rattlesnakes rattle less readily when smaller size (Kissner, Forbes, & Secoy, 1997), colder body temperature (M. P. Rowe & Owings, 1996), or the physical encumbrance of pregnancy (Kissner et al., 1997) renders them more vulnerable.

#### Rattling Is a Rich Source of Unritualized Acoustic Cues for California Ground Squirrels About Danger From Rattlesnakes

Rattlesnakes rattle at California ground squirrels for good reason. Even though northern Pacific rattlesnakes are a major predator of California ground squirrels, these snakes eat primarily young California ground squirrels (Fitch, 1949). Rattlesnakes are unable to kill adult squirrels because these squirrels have, under selection from rattlesnake predation, evolved the ability to neutralize rattle-

snake venom. Rattlesnakes can, however, kill and eat pups because the pups' small size limits the quantities of venom the pups can neutralize (Poran, Coss, & Benjamini, 1987). In part because of their reduced vulnerability to rattlesnakes, adult squirrels can be quite assertive in defense of pups. So, when rattlesnakes rattle at adult squirrels that are harassing them, the snakes are not rattling at their prey; they are rattling at the aggressive defenders of their prey, the parents of the pups the snakes seek. Similar dynamics have been reported for at least one other interaction between rattlesnakes and their mammalian prey: adult mountain cottontail rabbits (*Sylvilagus nuttalli*), which in defense of their young, approach and pounce on rattlesnakes (*Crotalus viridis*), which rattle in response to such harassment (Brown, 1990).

The confrontive interactions that take place between adult California ground squirrels and rattlesnakes can be quite prolonged, lasting from a few seconds up to several hours and occasionally extending across several days (Hennessy & Owings, 1988; Owings, in press). Such prolonged interactions combined with the antiquity of this predator-prey relationship (Coss, 1999) have set the stage for the evolution and development of assessment and management systems for use in snake-squirrel confrontations (Swaigood, Owings, & Rowe, 1999; Swaigood, Rowe, & Owings, 1999). As a result, rattling at squirrels has apparently become part of an exaptive (Gould & Vrba, 1982) communication system. The assertiveness and relative resistance of adult squirrels to venom have favored rattling by rattlesnakes at squirrels even though rattling probably evolved to deal with species that are predators on these snakes, not prey. Rattling is useful to the snakes because it apparently halts a squirrel's confrontation at least in the short term, as described above, and this pause may provide the squirrel with a useful moment of assessment. Confrontation by squirrels may also promote assessment because it evokes rattling. As we describe below, this sound is rich with acoustic cues that squirrels can use to assess the danger posed by rattlesnakes. These acoustic cues are often more useful than visual cues because many squirrel-snake encounters take place in the darkness of the burrows that house squirrel pups (Coss & Owings, 1978; Hennessy & Owings, 1988; Hersek, 1990).

The ground squirrels' use of acoustic cues in the rattling sound illustrates both the active, opportunistic nature of assessment processes and the contingent nature of some features of the Umwelt. Rattling probably did not evolve to manage ground squirrel behavior, but the squirrels have nevertheless put the sound to use in dealing with rattlesnakes. In addition, the cues in rattling exploited by ground squirrels are by-products, not formalized features of the rattling sound. Finally, these acoustic cues are available to squirrels only if the squirrels behave assertively enough to evoke rattling (M. P. Rowe & Owings, 1978, 1996).

The danger posed by rattlesnakes varies with both the size and the body temperature of these predators (M. P. Rowe & Owings, 1990). Adult rattlesnakes vary substantially in size because they grow throughout their adult lives, in contrast to birds and mammals. Larger snakes are more dangerous because they can strike farther and faster, leave their fangs embedded longer, and inject more venom than smaller rattlesnakes (Hayes, 1991; Kardong, 1986; M. P. Rowe & Owings, 1990). The body temperatures of rattlesnakes are also quite variable because snakes regulate body temperature more through exogenous than endogenous heat, again in contrast to birds and mammals. As a rattlesnake heats up, the

biochemical processes that support behavior speed up. As a result, warmer snakes are more dangerous than cooler snakes because they strike with shorter latency and higher velocity as well as with greater accuracy (M. P. Rowe & Owings, 1990). Some of the same factors that influence the danger posed by rattlesnakes also affect properties of the rattling sound. More dangerous, larger rattlesnakes have larger rattle segments and tail-shaker muscles and as a consequence produce rattling sounds of lower overall spectral frequency (see Figure 2) and higher amplitude. More dangerous, warmer snakes shake their rattles at higher rates, producing rattling sounds that are higher both in click rate (see Figures 3 and 4; as well as M. P. Rowe & Owings, 1996) and power (M. P. Rowe & Owings, 1996). Playback studies of rattling sounds have shown that California ground squirrels use the acoustic cues associated with rattlesnake body size and temperature (M. P. Rowe & Owings, 1978; Swaisgood, 1994; Swaisgood et al., 1999). In both field and laboratory studies, these squirrels behaved more cautiously in response to the sound of large rattlesnakes rather than small rattlesnakes; in the field, they exhibited more vigilance and tail flagging to the rattling sounds of warm rattlesnakes rather than cold snakes.

Some features of the rattling sound and its deployment by rattlesnakes may reflect the ongoing nature of the dynamic between the assessment and the management systems of rattlesnakes and their adversaries. For example, the two features of the rattling sound that covary with snake body size, that is, amplitude and dominant spectral frequency, increase logarithmically with body mass (M. P. Rowe & Owings, 1996). This suggests that size assessment by adversaries may have selected for the ability to sound large as early as possible in life, favoring relative growth rates in rattle segments and tail-shaker muscles that are higher than overall rate of growth. In addition, the human species may have imposed selection on the deployment of the rattling sound. Western diamondback rattlesnakes living in areas in which these snakes

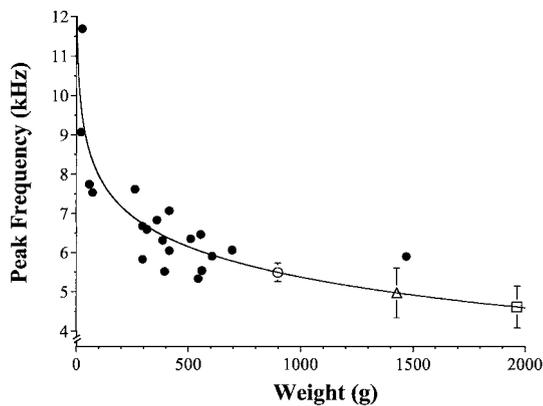


Figure 2. Exponential regression illustrating the significant ( $p < .01$ ) inverse relationship between the size of a rattlesnake and the dominant or peak frequency of that snake's rattling sound. Data ( $n = 20$ ) are from M. P. Rowe and Owings' (1996) study of northern Pacific rattlesnakes (frequency =  $-2.59 \times \log\{\text{weight}\} + 13.15$ ;  $r = .85$ ). Also plotted on the regression line is the average peak frequency (+ SE) of the various owl hisses. Open circle = little owl food-begging hisses ( $n = 6$  owls); open triangle = burrowing owl defensive hisses ( $n = 6$  owls); open square = burrowing owl food-begging hisses ( $n = 6$  owls).

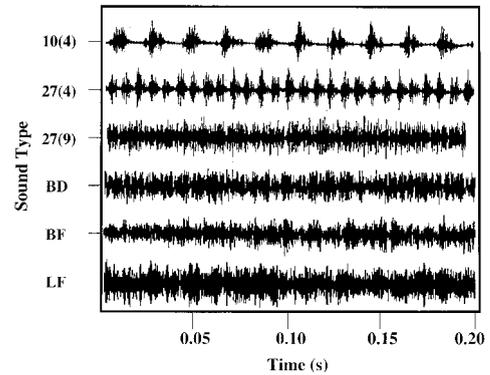


Figure 3. Expanded time waveforms of six sounds. 10(4), 27(4), and 27(9) = rattling by rattlesnakes at body temperatures of 10 °C and 27 °C, and with rattles either 4 or 9 segments long. The same snake provided 10(4) and 27(4). Notice that the long (9 segment) rattle string produces a sound in which individual pulses overlap, much like what occurs in the hisses of the owls. BD = burrowing owl defensive hiss; BF = burrowing owl food-begging hiss; LF = little owl food-begging hiss.

are intensively hunted by humans are less likely to rattle at humans than individuals of the same species living where snakes are subjected to only moderate levels of hunting (Fincher & Duvall, 1998).

#### Burrowing Owls Mimic the Sound of Rattlesnakes

It is likely that the assessment rule of thumb used by California ground squirrels, that sibilant sounds signal danger, is widespread among ecological associates of rattlesnakes. If this is true, then this rule of thumb is widely available as a communicative resource potentially exploitable as a management tool by third parties (as in

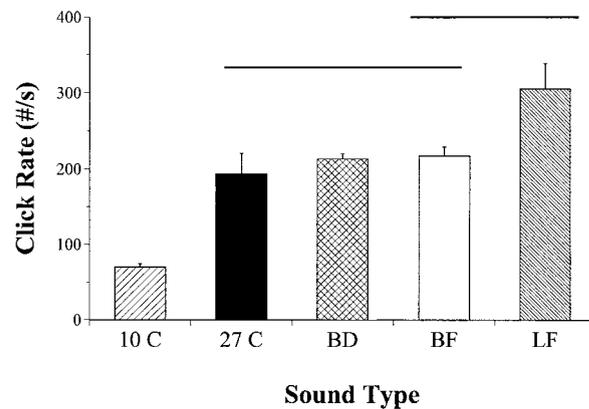


Figure 4. Mean (+ SE) of the pulse rates that make up the five categories of sounds. Click rate is expressed as number of clicks per second. Values for each animal were averages of multiple samples. Main effect for type of sound:  $F(4, 28) = 16.53$ ,  $p < .01$ . All groups overscored by the same line failed to differ from each other at the .05 level of significance using Tukey's honestly significant difference. 10 C and 27 C = rattlesnake rattling at body temperatures of 10 °C ( $n = 7$  snakes) and 27 °C ( $n = 7$  snakes). BD = burrowing owl defensive hiss ( $n = 6$  owls); BF = burrowing owl food-begging hiss ( $n = 6$  owls); LF = little owl food-begging hiss ( $n = 7$  owls).

Markl, 1985). The defensive hiss of burrowing owls provides an example of such exploitation; this hiss has long been known to sound very similar to the rattling sound of rattlesnakes, at least to the human ear (Garman, 1882; see also Figure 1). Confirmation that the burrowing owl hiss mimics the rattlesnake rattle would provide an example of acoustic Batesian rather than Müllerian mimicry, because these small owls are unlikely to be a serious threat to the animals they hiss at. In Batesian mimicry, a relatively harmless species gains protection by mimicking a harmful species. In contrast, in Müllerian mimicry, two noxious species each may gain additional protection by mimicking each other (Wickler, 1968).

We used two different methods to test the Batesian mimicry hypothesis (M. P. Rowe, 1984; M. P. Rowe, Coss, & Owings, 1986). The first method was a survey of the defensive sounds of owls to explore whether such vocal defensive hisses were generally characteristic of the relatives of burrowing owls (family Strigidae) or were specific to those species with a close ecological association with rattlesnakes. The second method used California ground squirrels as a bioassay in a playback study involving burrowing owl hisses, rattlesnake rattles, and control sounds.

Our survey of the defensive sounds of owls revealed that short, expirational hisses in defensive contexts are common in the strigids, but only burrowing owls in this family produce loud, long defensive vocal hisses. Inclusion of this vocal defensive hiss in the repertoire correlates with the presence of danger from rattlesnakes with regard to both microhabitat and broad geographic scale. Burrowing owls are the only strigid that both nests below ground, exploiting the same burrows and kinds of burrows that rattlesnakes do, and has a geographic distribution that overlaps extensively with that of rattlesnakes (M. P. Rowe et al., 1986). So, burrowing owls should encounter many predators that are concerned about rattlesnakes, and the assessment systems of those predators could be a source of selection for mimicry by burrowing owls. In contrast, the closely related Eurasian little owl (*Athene noctua*) is sympatric with vipers that do not rattle but not with rattlesnakes. Even though little owls often nest in rabbit burrows and (like burrowing owls) encounter fossorial or digging mammalian predators, little owls do not hiss vocally when cornered in their den—they produce a “kek kek kek kek” call (M. P. Rowe, 1984; M. P. Rowe et al., 1986).

Our use of California ground squirrels as a bioassay of the mimicry hypothesis was based on the following reasoning. Wild-trapped ground squirrels from populations currently experiencing rattlesnake predation should have picked up the association between rattling sound and danger. Such squirrels should behave cautiously in the presence of rattling sounds and of other sounds that they perceive to be similar to rattling. In contrast, squirrels that are wild trapped from a population not currently experiencing rattlesnake predation should not treat rattling or similar sounds as cues of danger. Squirrels from two such populations were exposed in the laboratory to playbacks of four different sounds (see Figure 1): rattling by a large, warm northern Pacific rattlesnake, hissing by a burrowing owl, white noise (similar in its sibilance to the previous two sounds), and a burrowing owl scream chatter. The scream chatter was included as a nonsibilant contrast to the sibilant rattle, hiss, and white noise playbacks. Additionally, the scream chatter allowed us to control for the possibility that squirrels perceive burrowing owls as dangerous. Scream chatters are used

by burrowing owls when mobbing their enemies and should be treated cautiously if squirrels are threatened by burrowing owls.

Each of these 8-s sounds was played back from inside a dark, simulated burrow just as the squirrel arrived at the threshold of this refuge while traveling along a runway from a start chamber. Five variables were quantified from video records of these trials (see Figure 5 caption). These variables were entered into separate principal-components analyses for each squirrel population, and each squirrel's score on the first component was entered into a single-factor, repeated measures analysis of variance, again separately for each population. The results provide strong support for the mimicry hypothesis (see Figure 5). In declining order, the rattlesnake-sophisticated squirrels treated the rattling sound as most alarming followed by the burrowing owl hiss, white noise, and scream chatter. The rattlesnake-naive squirrels did not differentiate among the sounds in any consistent way, exhibiting different patterns for different variables. Therefore, sibilant sounds are apparently not generally aversive; their aversiveness is most apparent for those squirrels associated with rattlesnakes. In addition, not all sibilant sounds are equal among rattlesnake-sophisticated squirrels; burrowing owl defensive hisses come closer to rattling than white noise in their aversive associations.

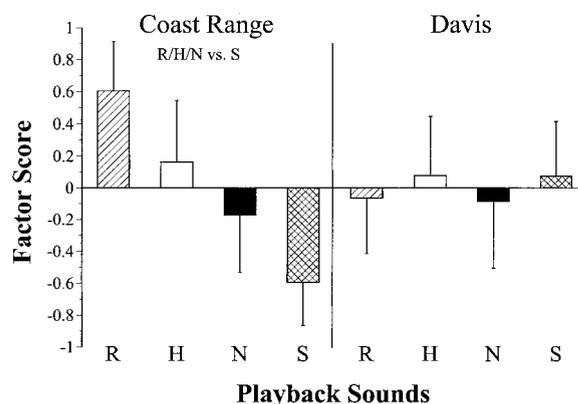


Figure 5. Mean standardized factor scores (+ SE) for Coast Range (rattlesnake abundant) and Davis (rattlesnake rare) populations of California ground squirrels ( $n = 8$  squirrels per population) for each of four playback sounds. Factor scores were from principal-components analyses of each squirrel population using the following five dependent variables. *Burrow entry*: squirrel either entered the sound-emitting artificial burrow or returned and remained in the release chamber. *Bipedal posture*: at least one bipedal alert posture during sound playback. *Distance from the artificial burrow*: distance of the squirrel (in centimeters) from the burrow entrance at the end of the 8-s sound playback. *Tail piloerection*: the change in maximum tail diameter before versus during playback. *Hesitation to leave runway*: percentage of the 8-s playback period that the squirrel spent in the runway rather than the artificial burrow or release chamber. All significant planned comparisons are shown above the graphs. Although response to N (white noise) was not significantly different from H (vocal defensive hiss from a burrowing owl) and R (rattling of a large, 850-g, rattlesnake), it was in univariate planned comparisons for tail piloerection and hesitation to leave runway. S = scream chatter from a burrowing owl.

## Ritualization: The Evolutionary Source of the Burrowing Owl's Mimetic Hiss

Tinbergen (1952) argued that many animal signals are derived activities, that is, activities that have evolved through modification of older behavioral patterns through a process called *ritualization*. Through ritualization, behavior may be modified in form, pattern, and circumstances of use as it is shaped by selection for communicative function. The concept of derived activities is a precursor to the concept of exaptation (Gould & Vrba, 1982) and complements one of the main points of this article. So far, we have argued that a key to the understanding of the form of a signal is identification of the properties of the assessment system or systems that it evolved to exploit. The concept of derived activities adds the point that researchers also need to know the form of the pattern from which the signal was derived.

The mimetic hiss of burrowing owls appears to have been derived from the spectrally similar food-begging call (see Figure 1; as well as M. P. Rowe, 1984). Unlike the mimetic hiss, the food-begging call is also used by closely related little owls (see Figure 1), which indicates that this call evolved before the mimetic hiss and is therefore a possible evolutionary source of the hiss. Remarkably, the food-begging vocalization is even preadapted for mimetic function, with spectral and temporal features that should be maximally intimidating to an animal that uses the rattling sound to recognize rattlesnakes. Like the mimetic hiss, the food-begging hiss emphasizes the low end of the frequency spectrum (see Figure 2), as the rattling sounds of large rattlesnakes do, and also has a high pulse rate, as the rattling sounds of warm snakes do (see Figures 3 and 4). The mimetic hiss may therefore have evolved from the food-begging hiss in part because some of its features preadapt it to sound like a large, warm rattlesnake. However, the

process of deriving the mimetic hiss from the food-begging hiss has involved more than a simple shift in the context of hissing, from a social-feeding context to a defensive one. The mimetic defensive hiss is significantly longer than the food-begging hiss, a change that has generated a closer match to the average duration of an episode of rattling by rattlesnakes (see Figure 6). Selection for mimetic defensive function may also have generated an increase in the amplitude of the defensive form of the burrowing owl hiss. Maximum intensities of the mimetic hiss range from 86 to 93 dB, which places it within the high-amplitude range of large rattlesnakes (around 90 dB) when measured 45 cm from both owls and snakes. However, no good measures of the amplitude of food-begging calls exist, so this remains a working hypothesis.

## Discussion

We have presented evidence that two ecological associates of rattlesnakes have exploited an aposematic signal, the rattling sound of rattlesnakes, in different ways. A prey species of these rattlesnakes, California ground squirrels, use their assessment systems to exploit rattling. These squirrels capitalize on incidental acoustic cues in rattling sounds that allow the squirrels to assess the danger posed by the rattling snake, gaining access to rattling through assertive confrontation of the snake. Burrowing owls use their management systems to exploit rattling; they defend themselves against mammalian predators by mimicking the sound of rattling. We have also presented evidence that the remarkable similarity between this burrowing owl defensive hiss and rattlesnake rattling is the product of both exaptation and adaptation. Food-begging hisses, the vocalizations from which mimetic hisses apparently have been derived, were preadapted to have the spectral and temporal features of the most dangerous, largest, and warmest rattlesnakes. But the evolutionary process of transforming food hisses into mimetic hisses has involved lengthening and perhaps amplifying these sounds, rendering them even more like the sounds of rattlesnake rattling.

The A-M approach to communication has helped clarify the thinking about the evolution of mimetic signals. It is the properties of the target's assessment system, not the model, that most directly shape the structure of the mimetic signal. This basic but underappreciated principle is revealed when researchers consider mimetic relationships in organisms whose sensory worlds are very different from that of humans. Many insects, for example, perceive ultraviolet light. Many insect-pollinated plants have, under selection from this ultraviolet sensitivity, evolved flowers with special areas, known as *nectar guides*, that are highly reflective of ultraviolet (UV) radiation (Romoser & Stoffolano, 1998). Fungi in the genus *Monilinia* induce nectar-guide mimicry in host plants as a part of their complex life cycle. This cycle requires that *Monilinia* spores, which develop on the leaves and shoots of their host plants, be transferred to the plant's flowers (Batra & Batra, 1985). The fungus causes infected leaves to wilt and take on a color that appears brown, bearing little resemblance (to the human eye) of the inflorescences required by *Monilinia* for its own reproduction. Nonetheless, the wilted areas are highly reflective of UV light, mimicking pollinators' perception of nectar guides, and attract these insects to the fungal spores the insects then transmit to the plant's flowers (Batra & Batra, 1985).

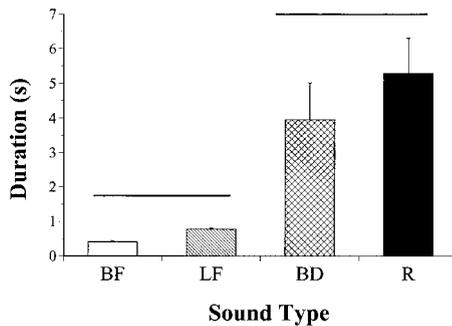


Figure 6. Average durations (+ SE) for owl hisses and rattlesnake rattling. Values for each animal were averages of multiple hisses or bouts of rattling. Main effect for type of sound:  $F(3, 17) = 11.15, p < .01$ . All groups overscored by the same horizontal line failed to differ from each other at the .05 level of significance using Tukey's honestly significant difference. Note that the durations of rattling shown here were elicited by looming at captive snakes. The mean duration of natural bouts of squirrel-elicited rattling (3.09 s) is also comparable with the mean duration of burrowing owl defensive hisses (3.96 s). This mean for rattling is based on five bouts recorded in the field from two wild rattlesnakes during natural encounters with squirrels. This sample size was too small for inclusion in our statistical comparisons. BF = burrowing owl food-begging hiss ( $n = 6$  owls); LF = little owl food-begging hiss ( $n = 6$  owls); BD = burrowing owl defensive hiss ( $n = 6$  owls); R = rattling from rattlesnakes ( $n = 3$  snakes).

The power exerted by assessment systems in shaping signals may also explain why some noxious species have aposematic displays that work through multiple sensory modalities, including vision, olfaction, and audition (e.g., moths in the families Arctiidae and Ctenuchidae, Dunning, 1968; Dunning et al., 1992; Dunning & Krüger, 1995; Rothschild, Moore, & Brown, 1984; Watson, 1975). Such multimodal input can expedite training of the predator's aversion to the aposeme and reduce the rate of extinction of the learned aversion (e.g., see Speed, 2000). Selection may also favor multimodal aposematic signals when the aposeme must deal with multiple potential predators with different perceptual specializations (cf. Owings & Hennessy, 1984). The bright colors of some arctiid and ctenuchid moths, for example, are most likely directed at visually hunting predators such as birds (Dunning, 1968; Watson, 1975), whereas the moths' ultrasonic warning sounds are targeted at sonar-hunting bats (Dunning, 1968; Dunning et al., 1992; Dunning & Krüger, 1995).

Similarly, different species of mimics of the same noxious model could use mimetic signals that are structurally quite distinct if they are targeted on different classes of "dupes" that cue on very different features of that signal. Such thinking may help account for the diversity within certain mimetic complexes, a perplexing phenomenon that has generated considerable review (Joron & Mallet, 1998; Mallet & Joron, 1999). Finally, selection arising from female mate choice has driven a shift of the aposematic signals used by arctiid moths to a courtship context. The ultrasonic pulses used to warn away bats, for example, have been co-opted at least four independent times for use in courtship displays (Simmons & Conner, 1996; Weller, Jacobson, & Conner, 1999).

### Future Directions

This review has raised a number of questions regarding the rattling sound of rattlesnakes, including the following.

1. How do predators of rattlesnakes, as contrasted with the prey discussed in this article, respond to the rattling sound?

2. What are the proximate processes whereby ecological associates of rattlesnakes come to avoid that venomous species? That task may be more challenging than it initially seems because rattlesnakes may have another nonvenomous Batesian mimic, gopher snakes (*Pituophis melanoleucus*). Gopher snakes resemble rattlesnakes in both general coloration and defensive behavior. When threatened, gopher snakes adopt rattlesnake-like S-shaped coiling–striking postures; produce sibilant sounds both vocally and through tail vibration; and spread their jaws, thereby adopting the triangular head shape characteristic of vipers (Kardong, 1980; Martin & Huey, 1971; Sweet, 1985). Studies of the closest relatives of California ground squirrels (rock squirrels, *S. variegatus*) indicate that learning plays a role in the ontogeny of discrimination between rattlesnakes and gopher snakes (Owings, Coss, Mckeron, Rowe, & Arrowood, 2001).

3. Does the rattling sound play a significant role in the development of this snake-species discrimination, and, if so, how?

4. Does the combination of rattling, assuming the defensive S-coil, and striking (Greene, 1988) make up a multimodal apose-

matic signal or do some of these features function as conditioned stimuli whereas others are unconditioned stimuli and/or modulators of the learning process (as in C. Rowe, 1999)?

5. What are the proximate details of the use of the mimetic hiss by burrowing owls?

6. How do potential predators of burrowing owls respond to their mimetic hisses?

Exploration of these questions should generate a wealth of new information on the dynamic between assessment and management processes.

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