

## Vibration and Animal Communication: A Review<sup>1</sup>

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**SYNOPSIS.** Vibration through the substrate has likely been important to animals as a channel of communication for millions of years, but our awareness of vibration as biologically relevant information has a history of only the last 30 yr. Morphologists know that the jaw mechanism of early amphibians allowed them to perceive vibration through the substrate as their large heads lay on the ground. Although the exact mechanism of vibration production and the precise nature of the wave produced are not always understood, recent technical advances have given answers to increasingly sophisticated questions about how animals send and receive signals through the substrate. Some of us have been forced to explore the use of vibration when all other attempts to manipulate animals in the field have failed, while others began to think about vibration to explain some of the puzzling behaviors of species they were studying in other contexts. It has thus become clear that the use of vibration in animal communication is much more widespread than previously thought. We now know that vibration provides information used in predator-prey interactions, recruitment to food, mate choice, intrasexual competition and maternal/brood social interactions in a range of animals from insects to elephants.

Studies of vibration in animal communication cast a small shadow in comparison with investigations into airborne signals and their interpretation. Yet, vibration perception as a sensory channel clearly predates that of the vertebrate ear mechanism. Extinct amphibians were able to detect vibrations through their jaw in contact with the ground, and conduction through the quadrate bone of the jaw to the inner ear via bony tissue (Hildebrand, 1995). A reduced hyomandibula associated with the quadrate in a fish's visceral skull evolved to form the ear ossicle called the stapes, or columella (Hildebrand, 1995). Even today, tetrapods that are in direct contact with the substrate over much of their body surface, such as non-anuran amphibians and reptiles, lack a tympanum and middle ear cavity. Caecilians, urodeles and some anurans, snakes, amphisbaenians and some lizards have a stapes, which may be attached to the shoulder girdle or skin, and are well suited to detecting low frequency vibrations from the substrate (Hildebrand, 1995). Thus, long

before the temporo-mandibular joint that gives humans so much pain freed up the articular and quadrate bones for new duty as ear ossicles, tetrapods had an apparatus in place for detecting substrate vibrations.

Massive ear ossicles are seen in large mammals that acquire acoustic information through bone-conducted vibration at the expense of auditory acuity at higher frequencies (Reuter *et al.*, 1998). For example, true seals have ossicles weighing from 160 to 320 mg, while the horse's ossicles weigh 74 mg, less than half that of the smaller seals. Elephants have massive ossicles with total weight in the Indian elephant of approximately 650 mg (Reuter *et al.*, 1998). Modern-day golden moles (family Chrysochloridae) have specialized structures for hearing low-frequency sounds emitted by their prey, including a complex hyoid apparatus in contact with their tympanic bulla, and many have massive ear ossicles (Mayer *et al.*, 1995). Frogs that are exceptionally sensitive to seismic stimuli appear to use the sacculus of the ear to detect these vibrations (Narins and Lewis, 1985), and sandfish lizards that use vibration to locate prey also have a very large sacculus (Hetherington, 1989).

Processing of vibrational signals by ani-

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mals does not require a traditional hearing pathway. Somato-sensory mechanisms are also well known (Kalmring, 1985): mechanoreceptors in sensillar hairs (Zachariassen, 1977; Kristensen and Zachariassen, 1980) and subgenual organs (Rupprecht, 1968; Bell, 1980a; Hutchings and Lewis, 1983; Kalmring *et al.*, 1997) of insects, basitarsal compound-slit sensilla of scorpions (Brownell and Farley, 1979a, b), and tricothoria and metatarsal lyriform organs of spiders (Barth, 1982). Snakes have simple nerve endings for vibration perception (Proske, 1969) and Herbst corpuscles in birds (Dorward and McIntyre, 1971) and Pacinian corpuscles in Eutherian mammals (Hunt, 1961; Calne and Pallis, 1966) allow for perception of vibrations. Gregory *et al.* (1986) found similar lamellated corpuscles in the legs of macropod marsupials, which suggests that these animals can detect ground-to-bone vibration produced by approaching predators. The blind subterranean mole rat, *Spalax ehrenbergi*, processes sensory information from vibrations produced by its head-banging neighbors through a somatosensory channel that is independent of the auditory mechanism (Nevo, 1990; Nevo *et al.*, 1991; Klauer *et al.*, 1997). Yet, they also lay their jaws against their burrow walls in a behavior that appears to enhance bony conduction of vibrations to their inner ears (Rado *et al.*, 1989, 1998). Whether or not both systems operate simultaneously is still under discussion (Rado *et al.*, 1998).

We know less about how large animals might produce vibration signals than how they might receive them. O'Connell *et al.* (1997) reported measurements of Rayleigh waves in the substrate that were propagated by elephant vocalizations and movements that might be important in long-range communication. Propagation of those signals was later quantified at distances up to 120 m (Arnason *et al.*, 1998).

Initiation of substrate vibrations during courtship has also been reported recently in vertebrates. The veiled chameleon, *Chamaeleo calyptratus*, produces plant-borne vibrations that may be used in communication (Barnett *et al.*, 1999). This is especially intriguing because Hartline (1971) noted thirty years ago that structures for

hearing in chameleons and snakes were at least superficially similar, and thus chameleons might detect substrate vibrations (Barnett *et al.*, 1999). Two species of frogs in the genus *Leptodactylus* produce substrate-borne vibrations, but in very different ways. The white-lipped frog, *L. albilabris*, produces Rayleigh waves as it sings a sexual advertisement call. This frog thumps its gular pouch against the soft soil where it lies and rapidly inflates its vocal sac (Lewis and Narins, 1985). Its Brazilian congener *L. syphax* has been observed drumming its forelimbs on granitic outcroppings, but this behavior is not produced simultaneously with either the advertisement or aggressive calls (Cardoso and Heyer, 1995).

Allopatric species of the genus *Dipodomys* footdrum in species-specific patterns (Randall, 1997). Banner-tailed kangaroo rats, *Dipodomys spectabilis*, produce individually distinct signatures in their footdrumming that remain constant over time (Randall, 1989) and that allow discrimination between neighbors and strangers (Randall, 1994). Although the airborne component of this footdrumming clearly does evoke a response when isolated and presented singly (Randall, 1994), Randall and Lewis (1997) have shown that these airborne signals are best for communication with distant neighbors while outside the burrow on windless nights. Substrate-borne vibration provides a channel for communication from inside the burrow to near neighbors on windy nights (Randall and Lewis, 1997).

Species-specific head drumming signals in the blind subterranean mole rat, *Spalax ehrenbergi*, may function as an isolating mechanism between species, as well as part of a long-range communication system within the species (Heth *et al.*, 1987). Individuals in tubes separated by a space of one mm could hear and smell each other but did not initiate drumming signals. When the tubes were brought into contact, individuals began head drumming that resulted in duets in 72% of the pairs tested. It is suggested that sensory input and signal response are both in the form of vibration in this blind subterranean species that would

have limited additional options for intraspecific communication (Rado *et al.*, 1987).

We know more about production and response to vibration in arthropods. Some of the best-known studies of vibration and communication are Friedrich Barth's work with spiders (Barth, 1998). Spiders produce vibration "... by drumming with the palps and the abdomen, by stridulating, or by plucking threads of their own or other spiders' webs" (Barth, 1982). Information from vibration in their environments affects many aspects of spider ecology: prey-catching, "... courtship, territorial behavior, and social interactions in species sharing a common web" (Barth, 1982). We have long known about spiders' ability to locate prey through vibrations of the web, but *Cupiennius salei*, a spider that does not live on a web, is also capable of reciprocal signalling between mates at least one meter apart on banana or agave plants (Rovner and Barth, 1981). Through use of synthetic male vibrations, Schüch and Barth (1990) showed that frequency and temporal characteristics of the male's signal were of utmost importance in female recognition, while amplitude was not. Females even compensate for the well-known changes in temporal parameters of the vibration with changes in temperature (Shimizu and Barth, 1996).

Workers of the leaf-cutter ant genus *Atta* produce both airborne and vibration components of a stridulation sound using a file-and-scraper mechanism (Masters *et al.*, 1983). When they are buried by a cave-in nest-mates do not respond to the airborne sound but rescue their buried relatives in response to the substrate vibration (Markl, 1967). The low frequency component of the stridulation output is emphasized underground, where radiation conditions are much better than in air for an animal of this size (Michelsen *et al.*, 1982; Masters *et al.*, 1983). Recent studies have shown that stridulations are also initiated to recruit workers to an attractive food source, and that these vibrations are transferred to the substrate through the ant's head (Roces *et al.*, 1993). Since the vibrations also mechanically aid the cutting process, it is thought that communication in this instance of foraging is a secondary effect for a pro-

cess that first increased efficiency in food handling (Tautz *et al.*, 1995).

Carpenter ants of the genus *Camponotus* drum with the mandibles and gasters to transmit a vibration signal over much longer distances than leaf-cutter ants (Fuchs, 1976). Responses to the vibrations are context-related and include more aggressive defense of the nest, as well as more rapid removal of dependent nest-mates (Fuchs, 1976). Hölldobler (1999) suggests that the drumming serves to elicit modulations in behavior by "influencing the motivational state of the receiver." In the genus *Aphaenogaster* of the southwestern United States, substrate vibration serves to amplify the pheromone signal first perceived by recruits, and they rush to move and conceal a food item (Hölldobler, 1999).

One of the most unusual associations is that between butterfly caterpillars and ants that protect them from predators (DeVries, 1990). Caterpillars produce secretions rich in amino acids and sugars that feed the ants, but they appear to attract the ants with vibration signals. DeVries (1990) suggests that the very common communication pathway known to ants is exploited by butterfly caterpillars and, based on comparative studies, appears to have evolved at least three separate times in related lineages.

Vibrations serve termites in pathogen alarm behavior. Termites bang their heads and produce substrate-borne vibrations as an alarm signal in response to a disturbance of the nest by predators (*e.g.*, Howse, 1964; Kirchner *et al.*, 1994). Young dampwood termites, *Zootermopsis angusticollis*, also produce a vibratory alarm in response to exposure to spores of a fungal pathogen. Unlike the disturbance alarm signal, the pathogen alarm induces nestmates to flee rather than move toward the stimulus source. Like a doomed human worker exposed to lethal radiation, the spore-exposed individual remains in place and signals to nestmates at a rate dependent on the concentration of spores encountered (Rosenhaus *et al.*, 1999).

My own interest in vibration was initially generated as I tried to manipulate male prairie mole crickets (*Gryllotalpa major*) in their burrows with airborne signals. Males

were sensitive to vibrations in the soil set up by footfalls, but they completely ignored airborne signals. In *G. major*, the vibrations are a component of the sexual advertisement call used to attract flying females and may represent bimodal communication important in male-male spacing (Hill and Shadley, 1997). This behavior, where vibrations targeting males are initiated along with an airborne sexual advertisement call targeting females, has a remarkable analog in the white-lipped frog, *Leptodactylus albilabris* (Lewis and Narins, 1985). Male bushcrickets (*Tettigonia cantans*) produce both sound and vibration as they call from plant stems, but the vibration, mainly in the form of bending waves, seems to play a role in mate location rather than competition with other males (Keuper and Kühne, 1983). These vibrations may also serve to reinforce acoustic signals (Latimer and Schatral, 1983).

Vibration can provide a channel of communication between males and females during mating when no airborne sound is produced. Male *Balamara gydia*, an Australian cricket, have a complete stridulatory apparatus but communicate with females by tapping their abdomens on vegetation. Both sexes tap, but neither has a tympanal organ (Loher and Dambach, 1989). Primitive male Australian gryllacridids, which are wingless, drum the substrate with tarsal elements of both hindlimbs and females respond in a duet (Field and Bailey, 1997). The New Zealand tree weta (*Hemideina femorata*), which can be as large as a small mouse, produces vibrations used in mate location by sending bending waves through the sturdy manuka tree (McVean and Field, 1996). Southern green stink bug (*Nezara viridula*) females from Ethiopia produce vibrations in plant stems that are used by males to locate them (Cokl *et al.* 1999). Cokl *et al.* (2000a) have recorded and analyzed four different kinds of substrate-borne songs and compared them for differences among populations from Brazil, Florida, Italy and Slovenia, as this species has become a world-wide pest. Interestingly, the courtship songs of both males and females in all four populations were not different, but the calling songs were different

in some features and may be the source of reported reproductive isolation among populations (Cokl *et al.*, 2000a, b). Black-horned tree crickets (*Oecanthus nigricornis*) in Canada produce percussive vibrations in plant tissue between a mating pair during courtship and after mating (Bell, 1980a), and the quality of their signals is dependent on the species of plant on which they are courting (Bell, 1980b). Male rice planthoppers (family Delphacidae) in Japan respond to vibrations produced by female abdominal vibrations by moving toward them (Ichikawa, 1976). The males respond with vibrations produced by tymbal organs, and these alternating vibrations of both sexes appear to transfer species-specific information required for mating (Ichikawa, 1976). The related leafhopper, *Graminella nigrifrons*, appears to use behavioral adaptations to overcome physical constraints imposed by substrate-borne signalling. Males use a call-fly strategy until they detect the response of a receptive female, and then they search for her by moving toward the light (Hunt and Nault, 1991). *G. nigrifrons* females use components of the male's vibration signal for mate recognition but probably not as a mechanism of female choice (Hunt *et al.*, 1992). Bending waves transmitted through plant tissue allow these animals to send and receive signals that retain specific characteristics over distances of meters (Michelsen *et al.*, 1982).

The deathwatch beetle, *Xestobium rufovillosum*, drums on the substrate. Males tap with their heads and then search for responding females. They increase activity in response to female tapping and turn repeatedly in the absence of response; although, in controlled experiments males were not able to locate females quickly (Goulson *et al.*, 1994).

The African tok-tok beetle (*Psammodes striatus*) taps its abdomen on the substrate and is able to locate females with approximately 10% of the energy that would be required to do a walking search (Lighton, 1987). Stone fly (Order Plecoptera) males and females tap the substrate with their abdomens in alternating patterns (Rupperecht, 1968) that are distinct enough to yield data useful in phylogenetic studies (Szczytko

and Stewart, 1979; Zeigler and Stewart, 1985). Males of the tenebrionid, *Eupsophulus castaneus*, tap with their abdomens in aggregations around UV lights in the southwestern United States. Since females do not tap, and since the sex ratio at the sites is 3:1, it is suggested that the substrate tapping might be a form of sexual advertisement in a lek system, or that it could play a role in male-male spacing (Slobodchikoff and Spangler, 1979). The East African desert tenebrionid beetle (*Phrynocolus somalicus*) taps its abdomen against a substrate of eroding sandstone (Zachariassen, 1977), and both males and females produce similar sounds (Kristensen and Zachariassen, 1980). Since there appears to be no mechanism to discriminate sex of the tapper from components of the signal alone, the vibration serves to attract members of the same species, and identification of sex takes place at closer quarters (Kristensen and Zachariassen, 1980). Male tenebrionids, *Eusattus convexus*, from Texas rap their abdomens on a substrate after physical contact with females, and often rap on the head or abdomen of the female (Pearson and Allen, 1996). Three species of tentyrriid beetles (*Eusattus* spp.) tap the substrate with their abdomens. Only males tap, and tap rate tends to increase in the presence of females (Tschinkel and Doyen, 1976).

Short-winged female meadow katydids (*Conocephalus nigropleurum*) discriminate among tremulation signals of males to choose a larger male, even in the absence of a signalling male (DeLuca and Morris, 1998). Female wandering spiders (*Cupiennius getazi*) use vibration signals for mate recognition but not female choice (Schmitt *et al.*, 1994), but female wolf spiders (*Hydrolycosa rubrofasciata*) actively choose males based on their drumming rate (Kotiaho *et al.*, 1996). Drumming activity does predict male survival, and so females may use drumming rate as an indicator of male fitness rather than as an index of male body mass (Kotiaho *et al.*, 1996). Drumming has both acoustic and vibratory components in wolf spiders, and the relative importance of either of these has not yet been determined (Parri *et al.*, 1997).

In addition to communication during

courtship and reproduction, vibrations can transfer information among social groups, including sibling groups. Nymphs of the treehopper, *Umberonia crassicornis*, display a sibling-group alarm signalling when one is attacked by a predator. Their mother responds to the plant-borne vibration to defend her offspring, but she only responds to the group signal (Cocroft, 1996). The female in turn uses vibration to signal to her offspring at a low rate throughout the day, and these signals appear to play a major role in maternal care. By signalling through the plant tissue, mother and offspring can communicate outside the perception range of their most common predators (Cocroft, 1999).

A variety of information is transferred through substrate vibrations by the terrestrial crab (*Gecarcinus lateralis*) with different patterns for different behaviors (Klaaßen, 1973). The male fiddler crab, *Uca pugilator*, drums the ground with his large chela during courtship, especially at night when waving the chela is ineffective as a signal (Aicher and Tautz, 1990).

Vibration can be the vehicle of predator-prey interaction. The wandering spider, *Cupiennius salei*, uses vibration for both, responding appropriately to the context of the vibration signal (Schmid, 1997). The scorpion, *Paruroctonus mesaensis*, can interpret vibrations in sand to determine both direction and distance of prey species, while the burrowing cockroach, *Arenivaga investigata*, uses vibration to detect and avoid the approach of the scorpion (Brownell, 1977). The jumping spider, *Portia fimbriata*, a predator of spiders, uses aggressive mimicry by generating a context-specific repertoire of simulated vibration signals on the prey's web (Tarsitano *et al.*, 2000). Pupae of the spotted leafminer, *Phyllonorycter malella*, respond to broadband vibrations initiated by probing activity of the parasitoid wasp, *Sympiesis sericeicornis*, by defensive/evasive behaviors that deter the parasitoid about 10% of the time (Bacher *et al.*, 1997). Golden moles of Namibia use seismic cues to detect prey (Narins *et al.*, 1997) as does the sandfish lizard, *Scincus scincus*, of the Sahara (Hetherington, 1989). Both species are known to dip their heads

in the sand as they forage. The great gerbil, *Rhombomys opimus*, footdrums in a warning signal in the presence of predators. This alarm signal appears to function primarily to warn juveniles of danger, though it also serves to warn adults (Randall *et al.*, 2000). The banner-tailed kangaroo rat, *Dipodomys spectabilis*, drums in the presence of snakes, but the behavior appears to be more for individual defense and parental care than a group alarm signal (Randall and Matocq, 1997).

What are the commonalities in these diverse vibration-based behaviors? Is there a common theme running through the diverse animals that produce vibrations through abdomen tapping, head banging, footdrumming, etc.? Certainly these animals are sending and receiving signals through the substrate in environments where this mode is the most efficient and the most economical. Animals in closed burrows have limited options for receiving input through airborne signals, especially if conspecifics are also underground. Those with open burrows may more efficiently transmit information on location and sex of the individual through substrate vibrations to near neighbors, especially in a windy or otherwise noisy environment. Fiddler crabs that wave to attract females during the day use vibration to communicate at night. We see vibration being especially important in desert and prairie animals, and this may not merely be a factor of our having looked more closely at these environments.

Even humans may not be as remote from this world of communication through vibrations as we might believe. According to Luther Standing Bear,

“That is why the old Indian still sits upon the earth instead of propping himself up and away from its life-giving forces. For him, to sit or lie upon the ground is to be able to think more deeply and to feel more keenly; he can see more clearly into the mysteries of life and come closer in kinship to other lives about him . . .” (Standing Bear, 1933).

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