Chapter 7
Vibrational Communication: Spiders to Kangaroo Rats

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Abstract An amazing variety of animals communicate by vibrational signals. The behavior is common, diverse and occurs in multiple taxa ranging from spiders and insects to rodents and elephants. Production of vibrations is a mechanical event of stomping, tapping, drumming, rubbing surfaces together (stridulation) and trembling the body (trembulation) to transmit both airborne and seismic signals. Groundborne vibrations are transmit through a diversity of substrates, including soil, rocks, leaf litter and plant stems and leaves. Receptors for the signals consist of ears and mechanoreceptors in mammals and specialized structures in arthropods. Mate attraction is an important function of substrate-borne vibrations, which are often combined with visual displays in multimodal courtship displays. In spiders substrate-borne vibrations function as sexually selected signals of fitness. Besides attracting mates, insects use vibrations to communicate between parent and offspring, members of the social group, food recruitment and in predator defense. Substrate-borne vibrations also are important in predator–prey interactions. Footdrumming as a communication system is the most developed in territorial kangaroo rats (*Dipodomys*). The species specific drumming patterns can be complex, and the bannertailed kangaroo rat (*D. spectabilis*) drums individually distinct footdrumming signatures to communicate territorial ownership. Kangaroo rats also drum during competitive interactions and courtship. In the presence of snakes the kangaroo rats footdrum in individual defense to inform the snake the kangaroo rat is aware and will no longer be easy prey.

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1 Introduction

Animals ranging from mammals to worms have evolved as many unique ways to communicate by substrate vibrations as there are different taxa (See Hill 2008, 2009; O'Connell-Rodwell 2010 for comprehensive reviews of vibrational communication). Because substrate-coupled vibrations are not subject to the same constraints as airborne signals, very small animals such as spiders and insects are able to communicate using low-frequency signals via a substrate. With an estimated 195,000 described species of insects in at least ten different orders generating substrate vibrations, the potential for diversity is huge (Stewart 2001; Cocroft and Rodriguez 2005). Some familiar examples of insects that communicate with substrate-borne vibrations include ants, grasshoppers, crickets, katydids, cockroaches, stoneflies, booklice, true bugs, leafhoppers, lacewings, heelwalkers, stoneflies and caddisflies (Stewart 2001; Eberhard and Eberhard 2012). Besides attracting mates, insects use vibrations to communication between parent and offspring (Nomakuchi et al. 2012), members of the social group (Boucher and Schneider 2009), food recruitment and in predator defense (Hill 2008; Crocroft and Hamel 2010). In an unusual function, pupae of the Japanese rhinoceros beetle, *Trypoxlus dichotoma*, issue substrate-borne vibrations to deter conspecific larvae from burrowing into them and breaking their cells, which leads to death (Kojima et al. 2012). Crustaceans comprise another group of arthropods that communicate by seismic signals. Fiddler crabs drum (rap) the substrate with the lower base of their major claw (chelae) and with multiple pairs of walking legs (Taylor and Patek 2010). Recent research has revealed how spiders use their well developed adaptations for generating and sensing substrate vibrations in multiple ways (See below and reviews in Uhl and Elias 2011; Elias and Mason 2010).

Vibrational communication is also common in mammals. Rodents from at least three different families of fossorial (ground-dwelling) and seven families of semi-fossorial rodents communicate by vibrational signals (See review in Randall 2001). These signals function mainly in territorial defense, competitive interactions and predator defense. Substrate-borne vibrations are also a good way for burrow-dwelling, fossorial rodents (mole rats) to keep track of their neighbors (Rado et al. 1987; Narins et al. 1992). The generation of substrate vibrations has also been reported in elephant shrews (Rathbun 1979), 75 species of Bovidae, 46 species of macropodoid marsupials, two species of Camelidae, two species of Giraffidae, seven species of Cervidae and elephants (Caro et al. 2004; Rose et al. 2006; Randall 2010). Little is known, however, about the function of these behaviors.

2 Vibrational Signals: Drumming, Stridulation and Trembulation

Production of vibrations for communication is basically a mechanical event of hitting, stomping, tapping, drumming, rubbing surfaces together (stridulation) and trembling the body (trembulation) to transmit vibrations to a substrate to generate both airborne and seismic signals. Usually no special structures are required, and animals use what moveable body parts are available to them to produce the sounds. The most common structures are those used for locomotion such as feet and legs. Insects and spider also use other segmented appendages to generate vibrations, including antennae and pedipelps respectively. Mice and termites bang their heads (Hill 2008).

A spider's acoustic world consists of substrate-borne vibrations that can be produced in three different ways. Percussion, described in 12 different families of spiders, occurs when the animal hits an appendage against a substrate (footdrumming) or another appendage. 'Web plucking' behavior is included in this category (Uhl and Elias 2011). Stridulation, described in 34 families, is when an animal rubs two rigid body parts against each other. Tremulation occurs when an animal oscillates its body or appendages and the energy from the oscillation is transferred to the substrata through the animal's legs (Elias and Mason 2010; Uhl and Elias 2011). Insects generate vibrations similar to spiders.

Mammals produce vibrations by hitting feet, arms, legs and head against a substrate. The substrate is usually the ground, but it can also include tree trunks and the animal's own body as in the case of the mountain gorilla (Randall 2001, 2010). Mammals most commonly drum their feet to generate low-frequency vibrations transmitted through the ground and air. The behavior ranges from single foot thumps or stamps to striking the feet repeatedly in rapid succession. Larger mammals, such as ungulates, employ a single foot. They lift the forefoot to strike the ground suddenly with the hoof one or more times (Caro et al. 2004). Macropodoid marsupials strike the ground with one or both hind feet to produce single or double thumps (Rose et al. 2006). Elephants, *Elephas maximus*, *Loxodonta africana*, bang their trunks and feet on the ground (O'Connell-Rodwell et al. 2000, 2007). Elephants can produce low-frequency vocalizations at such high amplitudes that they couple with the ground and become substrate-borne (O'Connell et al. 2000).

Fossorial mole-rats in the family Bathyergidae communicate to conspecific inside the burrow by footdrumming vibrations (See review in Mason and Narins 2001). Another fossorial rodent, the Blind mole rat (*Spalax ehrenbergi*) (the genus is now *Nannospalax*), drums the flattened anterodorsal surface of the head on the roof of the burrow in response to vibratory signals from conspecifics (Rado et al. 1987). The European mole vole (*Microtus pyrenaicus*) drums with its front incisors, and water voles (*Arvicola richardsoni*) run on three legs simultaneously using one hind foot to scratch a flank gland and drum it on the substrate to deposit the scent (Randall 2010).

Kangaroo rats (genus *Dipodomys*) have the most elaborate drumming behavior of any mammalian species studied thus far. They drum their feet in species-specific patterns that diverge in four important ways: (1) the number of individual pulses (footdrums) grouped together to create a footroll, (2) the number of footrolls grouped together in a sequence, (3) the drumming rate (drums/s) and (4) the total number of individual drums (pulses) of the feet in a bout of drumming (Randall 1989, 1997) (Fig. 7.1). These bipedal rodents generate the drums by hitting their large hind feet on the ground. The bannertailed kangaroo rat, *D. spectabilis*, props

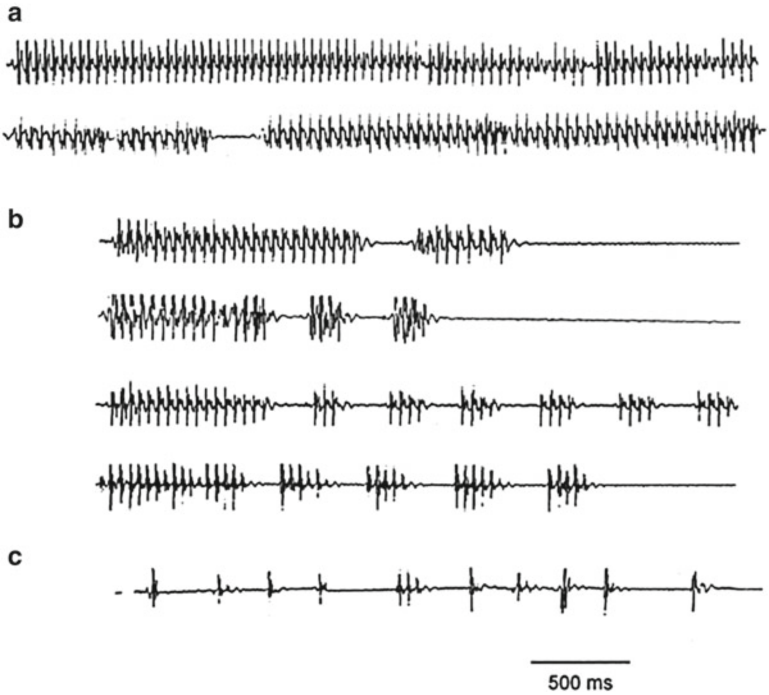

Fig. 7.1 Footdrumming patterns of three species of kangaroo rat (**a**) giant, *D. ingens*, (**b**) bannertailed, *D. soectabilis*, (**c**) desert, *D. deserti*

on its tail and hits the front of both hind feet together to generate a footdrumming signature consisting of a longer initial footroll followed by 1–12 shorter footrolls at an average rate of 17 drum/s. The giant kangaroo rat, *D. ingens,* alternates feet to generate 1–2 long foot rolls at 18 drums/s. The first footroll averages 69 individual foot-drums with the longest one recorded consisting of about 300 individual drums (Fig. 7.1) (Randall 1997, personal observation). The Heermanns kangaroo rat, *D. heermanni*, can produce several footrolls in a series at 20 drums/s (Shier 2003). The simplest drumming pattern in kangaroo rats is by the desert kangaroo rat, *D. desert*, with single drums at 0.25 s intervals (Randall 1997) (Fig. 7.1). Size is a limitation to drumming in kangaroo rat species. All species of kangaroo rats that communicate by drumming their feet have an average body size in excess of 60 g. Species weighing less than 60 g have not been observed drumming in any consistent way.

The bannertailed kangaroo rat also footdrums in the presence of snakes with modifications to the drumming signature (Randall and Matocq 1997). The kangaroo rats changes the two signal elements that account for the individual drumming signature: the number of footdrums in the first footroll and the number of footrolls in a sequence to make the footdrumming pattern less structured, more intense and longer.

Male wolf spiders, *Hygrolycosa rubrofasciata*, produce footdrumming signals during courtship. Although less complex, the spider's drumming signal shares some characteristics with the footdrumming signal of kangaroo rats. There are two main components of the spider's drumming signal: length (ms) and pulse rate (pulses/ms). A typical drumming bout lasts about 1 s with an average of 29 separate pulses. In comparison, kangaroo rats drum sequences considerably longer than 1 s, but the fastest drumming rate is much shorter (4–20 drums/s). Despite the simplicity of the drumming pattern of *H. rubrofasciata*, there are differences among the males. Pulse rate is highly repeatable within males so that individual males differ consistently from each, but the relative difference between males is small. Signal length and signal volume are also highly variable between males and repeatable for individuals. Females prefer the longer and more intense drumming (Rivero et al. 2000).

Although much less common than in arthropods and mammals, some species of amphibian use seismic vibrations to communicate. The white-lipped frog (*Leptodactylus albilabris*), with its body buried partially in the mud, produces seismic vibrations while vocalizing when the frog rapidly expands its vocal sac to generate a low-frequency thump as the sac strikes the substrate (Lewis et al. 2001). In contrast, calling male *L. syphax* beat their forefeet on the ground (Gridi-Papp and Narins 2010). Recently, toe twitching in frog and toads has been described and hypothesized to function as a vibrational, as well as a visual, lure to attract prey (Sloggett and Zeilstra 2008).

3 Substrates and Signal Transmission

Animals transmit vibrations through a diversity of substrates, depending on what is available in their habitat. A common substrate for transmission of vibrational signals by terrestrial vertebrates is the ground consisting of a variety of soils ranging from sand to clay. Energy is transferred through the ground in waves that vary in velocity and type with characteristics of the substrate (See Hill 2008 for review).

Among the substrates used to receive or transmit information by terrestrial insects, the stems and leaves of plants are the most widespread (Cocroft and Rodriguez 2005). Larger insects propagate vibrations along trunks and branches of trees (McVean and Field 1996). Aquatic insects and crustaceans transmit vibrations through the water (Hill 2008; Taylor and Patek 2010). Spiders send vibrations on webs they or another spider constructs, and bees communicate on honeycombs. These substrates have different transmission properties that must be taken into account when an animal wishes to maximize its ability to transmit information to a receiver (Cocroft et al. 2006; McNett and Cocroft 2008; Hill 2008; de Groot et al. 2011).

Recent research illustrates how the type of substrate can sharply affect the transmission and propagation of seismic vibrations and male mating success of spiders (Elias et al. 2004, 2010a; Hebets et al. 2008). Male jumping spiders, *Habronattus dossenus* Griswold 1987 (Salticidae), generate seismic signals during courtship on three different substrates in their environment: rocks, sand and leaf litter. Rocks and sand attenuate the signal, while leaf litter is the most favorable for signal transmission and mating success. Males, however, do not modify their courtship behavior to display only on the substrate with the best signal propagation, and they display on all three substrates as they encounter them (Elias et al. 2004).

Male wolf spiders, *Schizocosa*, display with visual and seismic signals on different substrates in their natural environments. *S. retrorsa*, court via drumming on their natural substrate of pine needles and red clay, where they experience the greatest mating success. They also court on leaf litter, where they are not normally found and have much lower initial mating success than on the natural substrates (Hebets et al. 2008). Rundus et al. (2010) found that *S. retrorsa* pairs, are equally likely to copulate in all signaling environments (Rundus et al. 2010). In contrast, *S. stridulans* normally inhabits leaf litter and courts females the most frequently there. Leaf litter transmits the vibrational signal the most effectively, and males are the most successful in obtaining copulations on the leaf litter. The substrate-borne vibrations are very important to mating success, because muted males unable to produce vibrational signals do not mate on any substrate (Elias et al. 2010b). Seismic feedback cues from female *S. stridulan* also affect where males court. Males that receive seismic feedback cues from females are more likely to optimize signal transmission by altering their use of signaling substrate than males without the feedback (Sullivan-Beckers and Hebets 2011). Another species of wolf spider, *S. ocreata*, occupies a complex microhabitat that includes leaf litter, wood, bark, soil and rocks. Mating success is the best on leaf litter, the substrate that has the best transmission properties for vibrational signals, and 85 % of successful matings occurred on this substrate. On substrates that attenuated seismic signals, males compensate by using more visual signals as a 'backup' (Gordon and Uetz 2011). Taken together, these studies demonstrate that male spiders exhibit flexible and opportunistic behaviors in their selection of substrates on which to generate vibrational signals during courtship. Although they may not always have access to the substrate that generates the best vibrational signal, they are able to compensate by seeking out a better substrate or by increasing the visual signals when on the substrates that limit the transmission of substrate-borne vibrations.

Insects also adjust vibrational signals to transmit well in their respective environments (Cocroft et al. 2006; McNett and Cocroft 2008). This response would be especially beneficial for plant-dwelling insects that are restricted to a single host. Plant stems and leaves, however, present limitations to signal transmission that could lead to mistakes in locating mates (McNett et al. 2010; de Groot et al. 2011). Because insects are much smaller than the structures on which they vibrate, the amplitude of the signal can be low and the vibrations dampened. The stems and leaves also are subject to wind-induced noise and act as frequency filters that can substantially alter the amplitude spectrum of a signal (Čokl et al. 2005; McNett et al. 2010). In contrast to the 3-dimensiononal space of airborne signals, vibrational signals are transmitted via a 1D environment on plant stems and a 2D space on leaf surfaces. Vibrational signals transmitted through plants in a 1D environment may carry very little, if any, information about source direction and distance (McNett et al. 2006; Čokl et al. 2007;

De Luca and Cocroft 2009) and lead to problems locating the source of the signal and mistakes in location of mates (de Groot et al. 2011).

Another accepted limitation to communication via substrate-borne vibrations in insects and spiders is that signal range is low and transmission is limited to a continuous substrate. A recent study demonstrated that the communication range of vibrational signals emitted by small insects is not limited to physically interconnected substrates. Grapevine leafhoppers, *Scaphoideus titanus*, are able to communicate between leaves on different cuttings up to 6 cm apart. Such signals may be detected by mechanosensory hairs or the Johnston's organ in the antennae (Eriksson et al. 2011).

4 Signal Reception

The diversity of animals that communicate by vibrations on multiple substrates has led to the evolution of diverse adaptations for signal reception. Animal "ears" consist of two basic types, pressure and mechanoreceptors. The mammalian ear, which is a pressure receptor highly specialized for reception of airborne vibrations, is the major receptor of the vibrations produced via footdrumming in both large and small mammals. Kangaroo rats and Gerbilline rodents have enlarged tympanic bullae and hypertrophied middle ear volumes specialized for hearing low-frequency airborne sounds that correspond to the frequencies in the drumming signal (Randall 2001, 2010). The use of drumming as a major signal modality may have led to ears better adapted to hear low-frequencies, because the bannertailed kangaroo rat has better low-frequency auditory sensitivity than a kangaroo rat species that does not drum, *D. merriami* (Shaffer and Long 2004).

Reception of seismic vibrations thorough an ear adapted to receive airborne vibrations led Randall and Lewis (1997) to ask the question: How does the bannertailed kangaroo rat with a well-adapted ear for hearing airborne sounds receive seismic signals? The kangaroo rats engage in footdrumming exchanges underground from burrows less than10 m apart, and kangaroo rats in the burrow footdrum in response to footdrums and disturbance on top of the burrow. The kangaroo rats apparently hear each other because they time their drumming responses not to overlap (Randall personal communication). A series of experiments revealed an answer to the question (Randall and Lewis 1997). Footdrums cause seismic vibrations that are transmitted directly through the ground from the site of drumming to the burrow wall and then radiated as an airborne sound into the burrow chamber. These vibrations are about 40 dB greater inside the burrow than airborne sounds outside the burrow. The kangaroo rats can use their sensitive ears for airborne reception of low-frequency sounds to hear the seismic signals when they become airborne in the burrow chamber.

Bone conduction is the usual route by which vibrations are transmitted to the inner ear of mammals. This may be a direct route to the inner ear through the cranial bones, or it may involve the middle ear. The blind mole rat, which is solitary and highly aggressive, receives information about the location of neighbors via seismic vibrations transmitted from their lower jaw pressed against the side of the burrow to the incus in the middle ear, thus bypassing the tympanic membrane (Rado et al. 1987, 1989). Blind mole rats may use somatosensory receptors to determine the direction of seismic vibrations in their tunnels (Kimchi et al. 2005). The massively hypertrophied mallei found in some golden moles is also an adaptation for receiving seismic vibrations by bone conduction. Although the human ear is highly specialized for reception of airborne sounds, another pathway of hearing could be through bone conduction via the skull to the sensory epithelium of the cochlea (Stenfelt and Puria 2010).

Snakes detect the substrate-borne vibrations via their mandible in direct coupling with the ground. Vibrations are transmitted from the mandible to the stapes via the quadrate bone to the inner ear (Young 2010). Much of the body of reptiles is in contact with the substrate, and mechanoreceptors in the skin are another possible avenue of vibration detection for these animals (Proske 1969).

Mechanoreceptors associated within deep skeletal structures such as joints and ligaments comprise another avenue of transmission of vibrations from the ground to the ear (Hunt 1961; Gregory et al. 1986). Pacinian corpuscles, which are pressure receptors consisting of lamellated bundles of cells, may transmit vibrations from the feet up through the legs and shoulders into the middle ear cavity or directly to the inner ear of placental mammals (Hunt 1961; Bouley et al. 2007). Kangaroos (Wallaby, *Thylogale billardierii*) have structures similar to Pacinian corpuscles in their legs (Gregory et al. 1986). The feet of elephants are rich in Pacinian corpuscles that could be used to detect ground-borne vibrations (Bouley et al. 2007), and the tip of the Asian elephant trunk is also rich in Pacinian and Meissner corpuscles, which may enable the elephant to detect very subtle vibrations with its trunk (Rasmussen and Munger 1996). There is no information on reception of seismic vibrations via the feet of kangaroo rats, but the possibility seems worth an investigation. The large hind feet of bipedal mammals provide a large amount of contact between the substrate and body. This coupling of the substrate with Pacinian corpuscles could act as a direct receptor of substrate-borne vibrations generated by footdrumming and facilitate reception of the seismic component of the signal.

Spiders are extremely sensitive to vibratory signals. Their main vibration receptor consists of slit sensory organs unique to spiders and found on virtually every part of the body, but especially legs and pedipalps (See comprehensive review of this system in Fratzl and Barth 2009). Slit sensilla are mechanoreceptors consisting of a hole in the cuticle of the exoskeleton covered by a membrane with a dendrite connected to the internal surface of the membrane (Hill 2008). These small grooves deform in response to mechanical stimuli imposed by movement and vibrations. The most sensitive of the slit sense organs is the metatarsal lyriform organ. Substrate vibrations cause the tarsus to move against the distal end of the metatarsus to compress the slits and stimulate the mechanosensory cells associated with them (Gingl et al. 2006). Spiders also use mechanosensitive hairs for seismic reception.

Insects have evolved a diversity of mechanoreceptors to receive substrate-borne vibrations (Hill 2008). The primary vibration receptors of insects are found in their legs. Campaniform sensilla, which are usually located near the joints, have comparatively low sensitivity, whereas the subgenual organ in the tibia is extremely sensitive. Its structure is complex and varies between different groups. Signals that are perceived by insects as substrate-borne vibrations also have a low intensity airborne component (Čokl and Virant-Doberlet 2003; Kavcic et al. 2013) that potentially may be detected over a few centimeters by antennal receptors (Kirchner 1994; Kavcic et al. 2013).

5 Footdrumming as Territorial Defense

Kangaroo rats use footdrumming as a mammalian version of individual acoustic signals to advertise territories analogous to bird song. In both birds and kangaroo rats, long range signals for territorial advertisement, rather than physical contact, communicate competitive ability and identity and minimize the cost of territorial defense (McGregor 1991; de Kort et al. 2009).

The bannertailed kangaroo rat is unique in its ability to generate individually distinct footdrumming signatures to communicate identity to territorial neighbors (Randall 1989, 1997) (Fig. 7.2). In playback experiments, territory owners footdrummed at higher rates in response to the footdrums of strangers compared with

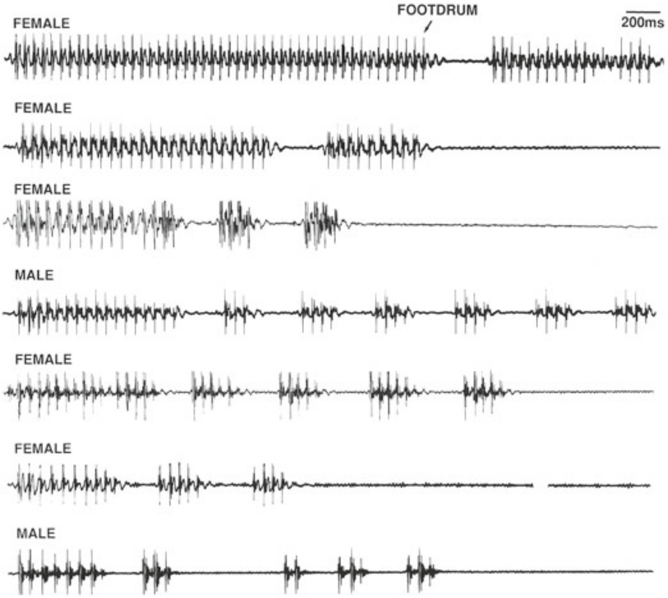

Fig. 7.2 Individual footdrumming signatures of adult male and female bannertailed kangaroo rat, *D. spectabilis*. Reprinted from Animal Behaviour, Vol 38, JA Randall, Individual footdrumming signatures in bannertailed kangaroo rats *Dipodomys spectabilis*, pp 620–630, 1989, with permission from Elsevier

neighbors (Randall 1993). Footdrumming signals of territorial owners differed the most from close neighbors compared with non-neighbors. Neighbor groups exhibited higher percentages of correct classification of footdrumming signals than non-neighbors (Randall 1995). The drumming patterns are flexible. The kangaroo rats can modify footdrumming signatures in response to changes in their social environment when they move into a new territory to distinguish themselves from their new neighbors (Randall 1995). This flexibility in communication is important to respond to constantly changing conditions of population density and proximity of neighbors. At higher densities, when there is more overlap of neighbors, more signal elements of the footdrumming signature are changed than in years when densities are low (Randall 1995).

In general, however, the individual footdrumming signatures of the bannertailed kangaroo rat tend to remain relatively constant from year to year. Adults that remained in the same territory had the most consistent footdrumming signatures. Of footdrumming signatures of 46 animals analyzed over two or more years, 37 % showed no change in the four structural signal elements (number of footdrums in the first, second and third footroll and footrolls in a sequence) while 63 % changed at least one signal element. Over the long term, however, no kangaroo rat radically changed its drumming signature. Kangaroo rats that drummed a long first footroll or a long footdrumming sequence continued to drum a long first footroll or footdrumming sequence with modifications, while kangaroo rats with shorter first footrolls and sequences also remained consistent within the general pattern (Randall 1995). The kangaroo rats possess the flexibility to alter drumming signatures to differ from new neighbors while still maintaining elements of their individual signature.

Greater variation in the footdrumming signatures of juveniles compared with adults suggests that young bannertailed kangaroo rats develop their individual drumming signatures as they mature (Randall 1995, 2010). The mothers' footdrumming provides an opportunity for young kangaroo rats in a litter (usually 1–3) while still in the burrow to learn the drumming patterns of their mothers during the 5–6 weeks before they begin to drum themselves. When about 0.25–0.50 % adult body weight, the young bannertaileds begin to exit the burrow to forage and footdrum at high rates (footrolls/h) (Randall 1984).

Do young bannertailed kangaroo rats copy the footdrumming signatures of their mothers? In a comparison of five signal elements of the drumming signatures of mother-offspring pairs, mother-daughter footdrumming signatures were similar, but the footdrumming signatures of sons tended to differ from their mothers. Daughters and mothers differed in one or less signal element while sons' footdrumming signatures differed on average from 2 to 4 signal elements from their mothers (Randall 2010). The reason for this difference is unclear, but it could lead to inbreeding avoidance (See discussion in section on mating).

Another highly territorial kangaroo rat, the giant kangaroo rat, *D. ingens*, drums individually distinct drumming patterns (Randall 1997). Whether the variation in the signatures communicates identity is less clear for *D. ingens* than for *D. spectabilis*. Although *D. ingens* footdrums in response to visual and auditory contact with neighbors, during playback tests in the field they footdrummed equally to playbacks of footdrumming from conspecifics and *D. spectabilis* and *D. deserti* (Randall 1997). A territorial signal can communicate "someone lives here" or "I live here". Kangaroo rats that drum single thumps, *D. deserti*, or simple patterns, *D. heermanni*, communicate that someone lives in the territory, but there is no information about identity (Randall 1997; Shier and Randall 2007). Thus far, only the bannertailed and giant kangaroo rats seem able to communicate identity via footdrumming signatures.

Invertebrates can use substrate-borne vibrations in territorial disputes similar to kangaroo rats. Larvae of the common hook-tip moth, *Drepana arcata* (Deoabiudea), detect approaching conspecific intruders by vibratory cues (Guedes et al. 2012). In response to the vibrations the larvae drum and scrape mandibles and anal "oars" against leaf surfaces in territorial defense. Territories consist of nests that require an energy cost to construct and are valuable to own. The drumming and scraping appear to mediate the encounters and allow the resolution of conflicts without physical harm, and the intruder usually responds by leaving the leaf (Yack et al. 2001). The vibrations are considered to be ritualized displays to warn another caterpillar not to waste time pursuing an occupied territory (Yack et al. 2001).

6 Vibrations in Multimodal Signals

Multimodal displays are favored by selection because they transmit more complete and reliable information to allow for faster and more accurate decisions. Many animals communicate using complex multi-component displays that contain signals or components made from different sensory modalities (chemical, visual, vibrational) (Partan and Marler 1999, 2005; Candolin 2003; Hebets and Papaj 2005; Taylor et al. 2007; Bro-Jorgensen 2009). Because researchers frequently study only one communication modality at a time, the complexity of signaling in animal communication has been under appreciated until recently. In terms of using vibratory signals in a multimodal signal, the best examples have been in spiders.

Jumping spiders, genus *Habronattus*, exhibit some of the most elaborate multimodal displays in the animal kingdom (Elias et al. 2012). The spiders employ sex-specific, colored ornaments that they coordinate with combinations of motion displays and substrate-borne vibrations. Vibrations consist of up to 20 elements organized in functional groupings (motifs) that change as courtship progresses, analogous to a musical composition. In a comparison of 11 species of *Habronattus*, Elias et al. (2012) found that displays ranged from no complex display (*H. borealis*) to a species with the most complex communication system yet described in arthropods. *H. coecatus* has 18 different morphological structures it can use as ornaments to combine with a diversity of vibrational patterns. Future comparative research on this diverse communication system in jumping spiders has a good chance to lead to a better understanding of the evolution of substrate-borne vibrations in complex multimodal systems.

The peacock spider, *Maratus volans*, is a charming example of another spider that combines vibrational and visual signals in elaborate, multimodal courtship displays (Girad et al. 2011). Males of this jumping spider from Australia unfurl a brightly colored flap that resembles the fan of a peacock, which they prominently displays while vibrating the abdomen by trembulation to produce substrate-borne vibrations. Three different types of vibrations are transmitted during the courtship in conjunction with the visual displays (Girad et al. 2011). The elaborate courtship of the peacock spider is unusual in its complexity. Besides being interesting to watch, the display might be a good model for studies of how female choice drives elaboration of sexually selected traits in spiders.

Seismic signals are also an important component of multimodal signals in wolf spiders, and their use varies among species. Male wolf spiders use both seismic and visual components of courtship displays that range from unimodal (seismic only) to multimodal (seismic and visual) (Hebets and Uetz 1999; Uetz and Roberts 2002; Uetz et al. 2009). Signal modes are species specific and can vary between even closely related sibling species (Hebets et al. 2013). The individual or complex components of multimodal signals interact to contribute to the efficacy of communication in many functional ways (Hebets and Papaj 2005).

Species of wolf spider in which females use mostly vibrational cues in assessing conspecific males tend to have vibration-based male courtship displays (*S. duplex* and *S. uetzi*) while the opposite is true for species in which females use more visual cues in male assessment (*S. stridulans* and *S. crassipes*) (Hebets and Uetz 1999). In a comparison of seven species of wolf spider (*Schizocosa* spp.), five of seven species of female preferred the vibrational to the visual signal. In the other two species the preference was equal (Uetz and Roberts 2002). When sibling species, *S. ocreata* and *S. rovneri*, were compared, females of both species detected multimodal stimuli faster than visual or seismic cues alone, but they differed in responses to cues once they became oriented (Uetz et al. 2009). In another species of wolf spider, *S. stridulans*, the seismic signal was sufficient for successful copulation, whereas the visual signal was neither necessary nor sufficient. Females preferred the more energetically expensive signal. In this example only the seismic signal is important for mating success, thus representing an example of a seismic signal dominating a multimodal communication system (Hebets 2008) Taken together, these results suggest multimodal signaling increases detection of males by females and that vibrational components are an important, and sometimes essential, part of the signal.

Although multimodal communication in mammals has not received as much attention or research as in arthropods, mammals often employ more than one signal modality in communication. Acoustic signals are often combined with visual. Wild chimpanzees drum on buttresses and trunks of trees to produce low-frequency sounds in environments of low visibility. The drumming occurs in discrete bouts that may be integrated into the chimpanzee's pant hoot as a multimodal signal for long distance communication (Arcadi et al. 2004). Drumming or thumping by ungulates is usually described as part of combination of visual and vocal signals when alarmed by predators (Caro et al. 2004). Red squirrels, *Tamias hudsonicus*, confront predators with loud vocalizations, stomping their hind feet and tail flicks (Digweed and Rendall 2009). Footdrumming accompanies visual and vocal signals in great gerbils (*Rhombomys opimus*) during mating interactions (Randall personal observations) and anti-predator behavior (Randall et al. 2000).

7 Vibrational Communication and Mating Success

For courtship signals to evolve, signals used during mating should convey honest information about male quality, be costly to produce, and be reliably detected and processed by female receivers (Zahavi 1977; Maynard-Smith and Harper 2003). Failure of a male's signal to stimulate a female's sensory system may cause serious fitness costs for the male (Guilford and Dawkins 1991). Females should prefer males with the more elaborate and energetic displays as a signal of male condition and fitness. High quality males are better able to afford the costs associated with the displays and their vigorous displays communicate to the female that she will have good genes for her offspring (Kotiaho et al. 1998). Furthermore, besides losing a mating opportunity, a male's survival may depend on his courtship performance. Female spiders can be very aggressive, and males that perform poorly may be in danger of becoming the female's next meal, and opportunity for future mating is eliminated (Elgar 1992; Prenter et al. 2006; Stoltz 2008; Roggenbuck et al. 2011).

The importance of vibrational signals in mating success and eliciting female receptivity is well established among numerous wolf spider species (Hebets and Uetz 1999; Uetz and Roberts 2002; Maklakov et al. 2003; Hebets 2005, 2008; Gibson and Uetz 2008; Sullivan-Beckers and Hebets 2011; Hebets et al. 2013). Variation in male vibration signals also influences female mate choice decisions in several other spider species (Kotiaho et al. 1996; Gibson and Uetz 2008; Soltz et al. 2008, 2009). Female choice in redback spiders*, Latrodectus hasselti*, is especially unambiguous. Females favor prolonged vibratory courtship that can last hours. Males attempting rapid mating without the prerequisite courtship pay a large cost. They are cannibalized before mating can be completed (Soltz et al. 2008). But this is not always the case. Sand-dwelling wolf spiders *Allocosa brasiliensis*, show a reversal in sex roles, and males sometimes cannibalize females of low body condition (Aisenberg et al. 2011).

Perhaps the best example of how drumming rate leads to mating success is the wolf spider, *H. rubrofasciata*. The extensive research on this species found that females prefer the most actively drumming males (Kotiaho et al. 1996), and males that drum at higher rates are selected by females over males with lower drumming rates (Kotiaho et al. 1996; Parri et al. 1997; Ahtiainen et al. 2004). During the short mating season (April–June) males drum while wandering around the habitat searching for receptive females. Once they locate a female the males increase the drumming rate to high intensity (Rivero et al. 2000). These high drumming rates are costly. They require large amounts of energy and compromise the immune function (Mappes et al. 1996; Kotiaho et al. 1998; Ahtianen et al. 2005). Males in better physical condition, therefore, are able to drum at higher rates than males in poorer condition (Kotiaho 2000), and females likely choose the high drumming males as an indicator of good genes for their offspring (Parri et al. 2002). These results demonstrate that production of substrate-borne vibrations via drumming are condition-dependent and function as honest signals of male quality in *H. rubrofasciata* (Kotiaho et al. 1996, 1998, 1999; Mappes et al. 1996; Alatalo et al. 1998).

Recent research demonstrates the importance of substrate-borne vibrations for female mate choice in another species of wolf spider (Wilgers and Hebets 2012). For male *Rabidosa rabida*, the seismic signal is critical for female mate choice. Males use both seismic vibrations and visual ornaments in mating interactions. When signals are separated, females respond to the seismic signal alone, but not to the visual signal. When females are able to detect both signal components, variation in visual ornamentation influences mate choice, and the females prefer ornamented males. These results suggest that the seismic signal of male *R. rabida* is necessary for female mate choice and that both the visual and vibratory components of the courtship display interact to influence female mating decisions (Wilgers and Hebets 2012).

Drumming in wolf spiders has a duel function. The males drum during courtship and in competitive interactions with other males (Delaney et al. 2007). In *S. ocreata,* signaling rates, which include foot tapping, are much higher in male–female interactions than in male-male contests and higher for males that successfully mated than for those that did not mate. Mean duration of some male displays is also greater for males that successfully mated. However, male size was not associated with probability of mating. Taken together, results suggest an intersexual selection context for the current function of male signals in these wolf spiders and that increased display vigor is associated with male mating success (Delaney et al. 2007). In contrast, in *S. lineatus* the presence of male vibrations was shown to stimulate females to mate, but had no other function (mate recognition and indication of mate quality) (Maklakov et al. 2003).

Female choice seems to be a driving force on the substrate-borne vibrations used in courtship displays of male jumping spiders. Mating success of *Phidippus clarus* males depends on signaling rate of the vibrations (Elias et al. 2005). These high intensity rates are correlated with male size, and both virgin and mated females assess male size through the courtship vibrations (Sivalinghem et al. 2010). Size is likely an important predictor of fitness in this species as larger, heavier males are more successful in male competition (Elias et al. 2008; Kasumovic et al. 2009).

Seismic feedback from females to courting males can be important for successful courtship. Males of the wolf spider *S. rovneri* court females with seismic signals transmitted through the forest floor. If females provide positive feedback with visual and seismic displays, males increase their overall signaling effort while males with no feedback maintain their signaling rates (Sullivan-Beckers and Hebets 2011). In addition, males receiving only seismic responses from females change the substrate on which they display (Sullivan-Beckers and Hebets 2011). These males have the flexibility to adjust their courtship behavior to optimize transmission of seismic signals and possibly obtain higher mating success.

Sometimes experience is a factor in female responses. In the pholcid spider, *Holocnemus pluchei,* females with previous mating experience generate substrate-borne vibrations most frequently. Intensity was higher in females that did not accept new copulations compared with those that copulated, and there was no difference in response to elaborate and non-elaborate courtship by males. Females probably communicate levels of sexual receptivity and may assess indirectly a male's ability to persist in courtship (Dutto et al. 2011).

Many insects communicate during courtship with substrate-borne vibrations (Hill 2008). For instance, when a female *Drosophila* senses vibrations generated by male abdomen shakes, she becomes receptive and stops walking. These abdominal quivers and associated vibrations, as well as their effect on female receptivity, are conserved in other Drosophila species (Fabre et al. 2012). In another recent example, treehoppers, *Enchenopa binotata* (Hemiptera: Membracidae), duet during mating interactions with plant-borne vibrational signals. A female's likelihood of responding to a male corresponds to the likelihood of her mating with him (Rodríguez et al. 2004, 2006). *Enchenopa* females are most selective when they experience vibrational signals with high variability. Females are adapted to adjust selectivity in response to the degree of variability in potential mates. The observed pattern of plasticity in mate preferences suggests that the benefits of selectivity increase as variability in potential mates increases (Fowler-Finn and Rodriguez 2012).

Footdrumming has been described during mating in rodents to function as a courtship signal performed in close proximity to the female. Fossorial mole-rats exchange footdrums during mating, including social *Cryptomys damarensis* (Jarvis and Bennett 1991) and the solitary Cape-mole-rat, *Georychus capensis* (Narins et al. 1992). Both the Mongolian gerbil, *Meriones unguiculatus* and great gerbils, *Rhombomys opimus*, engage in footdrumming exchanges during mating (Randall 2001, personal observation).

Bannertailed and giant kangaroo rats (*D. spectabilis* and D. *ingens*) footdrum during mating in intersexual exchanges. Neighborhood males enter the territories of estrous females on the night of mating, and females that would normally chase the male out of her territory instead engage in footdrumming exchanges. Males may drum softly as they approach a female and attempt to engage in contact. Many of these exchanges and mating occur in the burrow as the male and female move in and out of it. Females of both species exhibit less aggression toward familiar neighbor males and engage in more nonaggressive contact with close neighbors (Randall 1991; Randall et al. 2002).

The tendency of bannertailed kangaroo rats to mate with neighbors poses the danger of inbreeding. Both males and females are philopatric and continue to reside in their mother's natal territory for many months after weaning. When they do disperse, it is to a territory in their neighborhood or they may inherit the territory of their mother (Jones 1984; Waser et al. 2005). This dispersal behavior increases the likelihood that neighbors are related and that mating would occur between relatives. Molecular data show, however, that inbreeding is lower than expected if females were mating with their sons (Waser et al. 2005, 2012). Mother-son offspring were underrepresented in an analysis of long-term data of mating relationships, and offspring from first and second-degree relatives were also under represented to suggest that inbreeding does not readily occur and there is precopulatory mate choice (Waser et al. 2012). Waser et al. (2012) conclude that the kangaroo rats are more likely to discriminate kin by familiarity developed via association early in life than by spatial cues or phenotype matching.

There is some evidence to suggest that differences in footdrumming signatures between mothers and sons could be at least one mechanism of kin recognition and inbreeding avoidance in the bannertailed kangaroo rat. Sons develop footdrumming signatures to differ from their mothers while daughters and mother footdrumming signatures are similar (Randall 2010). If the kangaroo rats discriminate kin by familiarity developed via association early in life, mother-son pairs could learn to recognize each others' footdrumming signatures and avoid mating. Potential mates have ample opportunity to test for recognition of familiar footdrumming patterns during the vigorous footdrumming exchanges that occur during courtship (Randall 2010 and personal observation). Further study is necessary to determine why there are these sexual differences in learning footdrumming signatures. A comparison of paternity with footdrumming signatures might reveal whether males mate more frequently with unrelated females that have a different footdrumming signature from their mothers (Randall 2010). If so, this would be the first example of kin recognition by footdrumming signatures.

8 Vibrational Signals and Contest Assessment

Bannertailed kangaroo rat males compete vigorously for access to estrous females by footdrumming and chasing. Some of the longest and most vigorous footdrumming occurs during these contests. When the operational sex ratio favors males, up to six males may converge at the territory of the estrous female and compete for access to her (Randall 1991, 2010). A female is only in estrus a few hours, and males limit their total time in the female's territory to correspond with the time she is in estrus. Males footdrum and chase a majority of the time they are in the estrous female's territory, and when other males are present they drum at very high rates (1,128 ± 156.4 footrolls/h) (Randall 2010). Mating interactions in the giant kangaroo rat are similar. Footdrumming increases with the number of males present. The more males the higher the drumming rate (Randall 2010). In matings with two or less males, little footdrumming occurs, but when two or more males compete drumming increases exponentially (Hekkala 1995; Randall 2010). There is no evidence that the male that footdrums the most and longest has a mating advantage. Mating success seemed determined more by age than size (Randall 1991).

Because aggressive contests can be costly, assessment of fighting ability is important to competitors. The ability to sustain production of vibratory signals is probably a good predictor of fighting ability. Male jumping spiders, *Phidippus clarus*, use multimodal signals (visual and substrate-borne) to assess their fighting ability during aggressive encounters. Substrate-borne vibrations are important predictors of the winner, and heavier and more actively signaling males are contest winners. Furthermore, the duration of pre-contest phase is based on differences in vibration behavior between males. Bigger males are more willing to escalate towards contact phases even though the outcome of escalated fights is based made more on weight than on size (Elias et al. 2008).

Agonistic drumming activity of the wolf spider, *H. rubrofasciata*, is related to fighting ability (Kotiaho et al. 1999). *H. rubrofasciata* fights begin with agonistic drumming, and the winner of the fight drums at a significantly higher rate than the loser of the fight. About a third of the encounters were settled prior to escalation into a contact fight, probably by the difference in agonistic drumming rate between the opponents. Difference in agonistic drumming rate between the opponents was significantly greater than in those trials that did escalate to contact fighting. This suggests the spiders drum to transmit an honest signal of fighting ability, size and motivation.

Disputes in caterpillars (family Drepanidae) are solved by ritualized displays that are only used in territorial defense. The solitary larvae of the common hook-tip moth (*Drepana arcuata*) defend a silk nest on a leaf from conspecifics. They engage in ritualized "duels" with intruders, during which they produce vibrations by drumming and scraping their mandibles as well as specialized anal structures against the leaf (Yack et al. 2001). Most conflicts are resolved quickly, and the resident caterpillars generally wins the territorial disputes, but, relatively large intruders can displace a resident from its nest (Yack et al. 2001).

9 Predation

9.1 Predators Locate Prey

Predators are able to locate prey by responding to substrate-borne vibrations. They may respond to vibrations produced by some aspect of the habitat in which the prey is found or an incidental vibration from a natural activity such as eating (Hill 2008). The Namib desert golden mole, *Eremitalpa granti namibensis*, responds to incidental vibrations generated by motion of dune grass. The blind mole detects wind-caused vibrations of the grass transmitted through the sand and orients and swims through the sand to the source of the vibrations to hunt for termites associated with the grass (Lewis et al. 2006). Predatory stinkbugs (*Podisus maculiventris*) feed on caterpillars they locate by vibrational cues the prey makes when chewing plant material (Pfannenstiel et al. 1995).

Besides attracting mates, vibrational signals used in courtship attract predators (Parri et al. 1997; Ahtiainen et al. 2004; Lindstrom et al. 2006; Roberts et al. 2007). A recent study illustrates the importance of vibrational signals in sexual communication as a mode of prey detection by predatory spiders and provides a technique to analyze for predation events that cannot be observed readily in the field. Virant-Doberlet et al. (2011) used molecular techniques to analyze gut contents of the predatory tangle-web spiders, *Enoplognatha ovata* (Theridiidae), for the presence of leafhoppers as prey. Results revealed that leafhopper nymphs that signaled by plant-borne vibrations were preyed on at a greater rate than nymphs that were non-signaling. Playback experiments illustrated that the predatory spider used vibration signals to find their prey, and they killed significantly more displaying males than females. These results are important for two reasons. First, the innovative use of molecular techniques to analyze gut contents creates an opportunity to investigate previously untested predator–prey association, and second, the study demonstrates that exploitation of vibrational signals by predators may be important drivers of the evolution of predator–prey interactions (Cocroft 2011; Virant-Doberlet et al. 2011).

The ultimate predatory spiders that use vibratory deception to capture prey are in the family Salticidae, genus *Portia* (Nelson and Jackson 2012). They are jumping spiders that feed on other spiders using fascinating behavioral adaptations that minimize detection and identification by the prey and thereby prevent a counter-attack. *Portia* is unusual because it exploits a wide range of spider species by using a trial-and-error method (Jackson and Wilcox 1990). They capture prey by invading their webs and mimicking the vibrational signals of caught insects or approaching mates. *Portia fimbriata* masterfully mimics the behavior of an insect ensnared in the capture zone of a web by making faint vibrations on the periphery of the web. In webs of more dangerous, large prey *Portia* vibrates vigorously on the web to create a disturbance ("smokescreen") to mask its approach (Tarsitano et al. 2000).

A predatory strategy of the fringed jumping spider, *P. fimbriata*, is to imitate the vibrational signals of males to lure out females. *Euryattus sp*. females, another saltacid spider species, are unusual because they nest inside suspended rolled-up leaves. During courtship, *Euryattus* males perform a specialized vibratory display (shuddering) while standing on a suspension nest of a female, causing the leaf to rock back and forth. The female exits the leaf and either mates with the male or drives him away. *P. fimbriata* mimics the courtship display by standing on the leaf and shuddering in a similar vibratory displays to lure *Euryattus* females from their nests so they can prey on them (Jackson and Wilcox 1990; Nelson and Jackson 2012).

The predatory strategy of invading the webs of web-building spiders has been adopted by an insect predator, assassin bug, *Stenolemus bituberus*. The assassin bug plucks the silk to generate vibrations that mimic prey of the spider. The vibrations have a temporal structure and amplitude that is similar to those generated by prey and different from a courting male. If the spider ventures within striking distance of the plucking assassin bug, it becomes the bug's dinner (Wignall and Tayler 2011). The assassin bugs' problem is how to access the web and move close enough to ambush without alerting the prey, because web silk is extremely proficient at transmitting vibrations and web-building spiders have acute ability to detect vibrations on the web. To overcomes this difficulty the assassin bugs have developed a simple strategy to avoid detection. They use natural event of wind to function as a 'smoke screen' to mask their approach (Wignall et al. 2011).

There is ample evidence that snakes are capable of responding to substrate-borne vibrations (Young 2010). It is possible, therefore, that snakes could eavesdrop on the territorial footdrumming of kangaroo rats to locate them as prey, especially when they are very hungry after hibernation. Results of playback tests of gopher snakes, *Pituophis melanoleucus affinis*, to territorial footdrumming of the bannertailed kangaroo lend some support to this hypothesis. Six of six snakes that had not eaten for an indefinite period and were very hungry moved toward a buried, mechanical thumper playing territorial footdrumming and repeatedly struck at the kangaroo rat positioned on top of the thumper in a protective cage. In contrast, 5 of 7 snakes that had eaten within 4 weeks and were presumably less hungry moved away and avoided the territorial footdrumming, and only one snake struck at the kangaroo rat (Randall and Matocq 1997). There were mixed results with snakes that had not eaten in 6 weeks. Four approached and 5 avoided the thumper. Because hungry snakes often have to travel long distances to locate patchily distributed prey (King and Duvall 1990), it would be to a hungry snake's advantage to use the drumming to locate areas where they could wait in ambush for a kangaroo rat dinner.

9.2 Prey Fight Back

Predation is a strong selective force on the evolution of defense behavior of prey, and an appropriate defensive response is critical to survival. An unique example of an animal that responds to specific substrate-borne vibrations created by the approach of a predator is the red-eyed tree frog, *Agalychnis callidryas*. Egg-eating snakes attack the egg clutches that mature on vegetation hanging over a pool. Vibrations generated by the snake trigger an immediate synchronized response to propel the embryos from the egg capsule into the water below. The response by the frogs is very specific, and natural disturbances in the environment such as wind and rain do not trigger release of the embryos. This specificity is important because there is an abundance of predators in the pond below that will prey on the embryos, and immature embryos would be especially vulnerable (Warkentin 2005; Caldwell et al. 2009, 2010). Even caterpillar larvae (*Semiothisa aemulataria* (Geometridae)) can distinguish the vibrations generated from different sources. They defend themselves from specific predators by hanging on a silk thread in response to wasps (*Polistes fuscatus*) and stink bugs (*Podisus maculiventris*), but not in response to birds, other herbivores or abiotic factors (Castellanos and Barbosa 2006). The masked birch caterpillar (*Drepana arcuata*) does not respond to disturbances caused by wind and rain but does respond to vibrations caused by the approach of predators (wasps) and conspecifics (Guedes et al. 2012).

Sexually selected signals attract mates and provide an advantage in courtship, but they can also attract predators to cause a disadvantage in survival (Zuk and Kolluru 1998; Rosenthal et al. 2001). Animals using multimodal signals in courtship displays may be especially vulnerable. In spiders, the benefit of increased signaling efficacy of large visual ornaments and complex, multimodal signaling may be countered by increased predation risks. For instance, wolf spiders, *S. ocreata*, are more vulnerable to predation by jumping spiders (*P. clarus*) when the multimodal signal of both visual and seismic vibrations are used in mating displays than when there is only the visual signal (Roberts et al. 2007). Higher drumming rates during mating encounters attract predators. Female wolf spiders, *H. rubrofasciata*, will not mate with non-drumming males and prefer males with the higher drumming rates (Parri et al. 1997; Ahtiainen et al. 2004), but male spiders with higher drumming rates are more prone to predation by pied flycatchers (*Ficedula hypoleuca*) (Lindsrom et al. 2006). Because these males are in better condition and have higher mobility, they are able to escape predator attacks better than males with lower mobility. The males in good condition, therefore, can compensate for the predation risk generated by higher drumming rates and bear the energy costs and predation risks of signaling better than males in poor condition.

An interesting insect example is the response of ants to the vibrational alarm signals of insects that provide them with food. In this mutualistic association, the ants protect the prey from predators, the prey survive the approaching predator, and the ants are given nectar as food by the insect prey (DeVries 1990; Travassos and Pierce 2000). Adult treehoppers, *Publilia concava,* generate distinct substrate-borne vibrations in response to the approach of the ladybird beetles. Ants respond with increased activity that is interpreted as anti-predator behavior directed at the beetle (Morales et al. 2008).

Predation pressure is a strong evolutionary force that has led to a diversity of anti-predator behaviors in mammals. Small mammals, mainly rodents and elephant shrews, drum their feet in the presence of snakes (Randall 2001, 2010). A large number of hoofed mammals strike their feet on the ground when they encounter a predator (Caro 1995; Caro et al. 2004). Macropoid marsupials, kangaroos and wallabies, thump their feet when disturbed and in the presence of predators (Rose et al. 2006). Male and female adult eastern grey kangaroos, *Macropus giganteus*, generate loud thumps with their hind feet, Because solitary kangaroos thump more than grouped kangaroos, the thumps may function to startle a predator or to communicate it has been detected (Bender 2006). It seems surprising given the number of macropods that thump their feet and the commonness of the behavior that it has not been studied in more detail.

Kangaroo rats employ an active defense against snakes. After detecting a snake, territorial kangaroo rats (*D. spectabilis, D. ingens, D. deserti*) approach to within striking distance, jump back and begin to footdrum. The kangaroo rats often continue to approach a snake and footdrum until the snake leaves or is removed (Randall and Stevens 1987; Randall and Matocq 1997; Randall and Boltas King 2001). This would seem a very dangerous, non-adaptive behavior, but for kangaroo rats the drumming is adaptive because it functions as an individual defense to thwart further hunting by the snake. The kangaroo rats actually reduce risk to themselves by their apparently risky behavior. This conclusion was supported by experiments with bannertailed kangaroo rats and gopher snakes, *P. m. affinis* (Randall and Matocq 1997). In laboratory encounters gopher snakes decreased stalking behavior in response to increased footdrumming by the kangaroo rats. Snakes avoided footdrumming playbacks in field tests, unless they were very hungry (Randall and Matocq 1997). The drumming communicates to the snake, which hunts by surprising its prey in an ambush, “I am not easy prey so get out of my territory”, and in natural observations snakes did leave the territory (Randall and Stevens 1987). The hypothesis that the footdrumming in the presence of snakes is directed to warn adult neighbors was rejected because neighboring kangaroo rats did not respond to playbacks of the anti-snake drumming of a neighbor (Randall and Matocq 1997). Mothers, however, footdrummed at higher rates and came closer to the snake than nonmothers to suggest that the footdrumming warns vulnerable offspring in the burrow of danger.

Both social and solitary rodents drum their feet in the presence of predators (Randall 2001). The great gerbil, *Rhombomys opimus*, is a social rodent that lives in family groups consisting of an adult male, related females and their offspring (Randall et al. 2005). Adults and juveniles of both sexes emit alarm calls and footdrum in the presence of terrestrial predators (Randall et al. 2000; Randall and Rogovin 2002). This well-organized alarm system communicates degree of risk and response urgency to family members (Randall and Rogovin 2002). All alarm calling occurs out of the burrow, but when the gerbils footdrum they change the location of their drumming in response to the type of predator and its ability to enter the burrow (Randall et al. 2000). When a large terrestrial predator such as a fox or monitor lizard, *Varanus griseus caspius*, that is unable to enter the burrow is sighted, the gerbils vocalize and enter the burrow and footdrum from inside the burrow. In response to a sand boa, *Eryx miliaris*, that can enter the burrow, the gerbils footdrum outside of the burrow in closer proximity to the snake than when encountering either a wolf hound (represents a fox) or monitor lizard (Randall et al. 2000). Response to the snake suggests the gerbils may be communicating directly to the snake that its chances of ambush are thwarted much in the same way as in kangaroo rats.

10 Evolution of Vibrational Communication

The path of evolution of vibrational communication is unclear. We know that it is a very ancient system dating back in vertebrates to ancient amphibians (Hill 2008). Signaling by tremulation of the body or of some of its parts is one of the most widespread and, presumably, primitive modes of mechanical signaling in insects (Stritih and Ĉokl 2012).

We can only speculate about how vibrational signals originated in arthropods, but it seems logical that drumming, tapping and rubbing originated from incidental actions associated with walking. A slightly higher leg lift, louder foot step or accidental thump of the abdomen might capture the attention of a potential mate and eventually become part of a mating display. Females often have a preference for novel signals, and female jumping spiders, *H. pugillis*, prefer novel forms of seismic signals (Elias et al. 2006). The current diversity of communication by substrate-borne vibrations in arthropods illustrates a high radiation in which the behavior evolved multiple times at a fairly fast rate (Rodríguez et al. 2008).

Changes in habitat and its affect on mating signals may be a driving force in the radiation of some spiders and insects. Elias and Mason (2010) suggest that the diversity of substrate-borne, sexually-selected signaling in spiders, insects and other arthropods is associated with “sensory drive” mechanisms. This theory predict that females evolve preferences for mating signals that are efficiently detected and decoded (Endler and Bosolo 1998). The heterogeneity of spider habitats drives the modification of signal production for efficient signal transmission leading to evolution of female perception to match the changing signal leading to assortative mating and species divergence (Hebets et al. 2013). In a similar interpretation for insects, Cocroft et al. (2010) propose that plant host shifts led to divergence in mate communication systems in insects because differences in male advertisement signals of *Enchenopa* treehoppers covary with differences in resource use. Once differences in signal traits have appeared female mate choice is likely to reduce gene flow and promote further divergence (Cocroft et al. 2010).

The path of evolution of footdrumming as communication in mammals can only be speculated, but the diversity of mammals that drum suggests the behavior evolved independently in different lineages (Randall 2001). It seems logical to speculate that footdrumming or stomping in some lineages evolved from incidental behavior. A cow or horse stomping its feet when swarmed by flies on a hot summer day or a rodent or bird trying to dislodge a mosquito are familiar sights (Darbro and Harringron 2007). Deer mice, *Peromyscus maniculatus* stomp their feet in defensive behavior during attacks by biting stable flies, *Stomoxys calcitrans* (Kavaliers et al. 2005). Defensive responses to the biting flies are acquired through social learning, and observers learn faster when the demonstrator is familiar or related. This recognition of incidental signals that communicate threatening stimuli could become a precursors of anti-predator behavior through the social learning of fear-induced avoidance responses.

When mammals become excited and agitated by stressful situations, they may drum or stomp their feet (Randall 2001). Foot shock and novel stimuli induce drumming in Mongolian gerbils (Routtenberg and Kramis 1967), and footdrumming rates in kangaroo rats are especially high in stressful situations (Randall 1991; Randall and Matocq 1997). Drumming, therefore, could have originated from responses to stressful situations when animals become fearful in the presence of a predator or a competitor. The original drumming may have been a result of displacement behavior by a fearful animal in conflict about whether to chase or flee (Randall 2001).

Drumming also may have originated by ritualization of behavior associated with digging and running. The drumming could be an extension of digging in fossorial rodents where the digging becomes ritualized (Francescoli and Altuna 1998). Kangaroo rats often engage in a brief drumming bout of 2–4 drums before they chase another kangaroo rat. The behavior appears to be an intention movement to indicate a high probably of locomotion toward another animal. This behavior is seen in kangaroo rats that are too small in body size to drum in extended bouts for communication as well as in the larger territorial species (Randall 2001). Drumming to communicate territorial ownership evolved in the larger-sized kangaroo rats that overcame energetic limitations from size constraints (Randall 2001).

11 Concluding Remarks

Vibrational communication is an important mode of communication that requires more recognition and investigation. Although its diversity parallels or surpasses other communication modalities, a strong body of research has only recently begun to develop. Studies of vibrational signals have a very broad base because invertebrates and vertebrates use vibrational signals as a major modality of communication in both intra- and inter-specific communication in many different contexts. It is my hope that recent attention to vibrational communication in the comprehensive book by Peggy Hill (2008), an edited volume by Caitlin O'Connell-Rodwell (2010) and this review where I have included the latest research will generate the interest that the subject deserves and that a strong theoretical and empirical base for the behavior will be developed.

The diversity and sophistication of vibrational communication is quite interesting and surprising. Substrate-borne vibrations are the only mode of communication, with the possible exception of chemical, that can be accomplished by animals ranging from a simple caterpillar to an elephant. The idea that developing beetle pupae could signal conspecific larvae with substrate-borne vibrations to deter being run into or caterpillar larvae discriminate vibrations from different predators would not have been considered only a few years ago. Considering the large number of insect, spiders and mammals that communicate with vibrational signals in one form or another, there is still much to learn about many interesting adaptations for communication that involve these signals.

The diversity of how vibrational signals are produced and the substrates on which animals produce them is rather surprising. It seems animals can produce vibrational signals on almost any substrate, including water. For example, jumping spiders in Damian Elias's lab readily vibrate on flesh-toned pantyhose pulled over an embroidery hoop (Randall personal communication). The assumption should be avoided, therefore, that no communication is occurring because the substrate seems unlikely or there is no discernable sound. There are many substrates used by animals for vibrational communication that require investigation. Much more is to be learned about transmission properties, behavioral preferences for types of substrates and the mechanisms for the choice.

The importance of and variation in vibrational signals used in mating behavior has become well established in arthropods. We find the flamboyant sexually selected signals of spiders of great interest. There is strong evidence that female choice in spiders is related to the intensity and duration of drumming and other substrate-borne vibrations generated by courting males. These vibrations are sexually selected signals that are probably under intense selection for honesty, especially considering that female spiders are able to attack and kill males that have not communicated effectively. This picture of spider mating, however, is based on only a few species, and there are examples of role reversal. The task ahead is to learn about mating behavior in many more species from different locations and habitats if comparisons of different mating tactics are to be good models for understanding the evolution of the behavior.

Evidence for vibrational signals as important component of multimodal signals in insects and arthropods is becoming well established. Unfortunately, the same cannot be said for mammals. Seldom is the foot stomping or drumming a focus of an investigation. Often the act of drumming is treated as an incidental occurrence and not studied as a component of behavior. For instance, we know that many ungulates drum or stomp a foot when alarmed, but the reason for the behavior and what is communicated remains to be studied in any detail. The same is true for macropoids. Despite the description of drumming in multiple species of kangaroos, there has been little effort to study them in any detail. The only mammal where a complete picture of drumming as communication has been established is in kangaroo rats.

One reason that the field of vibratory communication did not advance until recently was the lack of ability to "hear" and record the signals for analysis. Within the past 10 years the vast world of vibratory communication in small invertebrates has been discovered with sensitive instruments such as the laser Doppler vibrometers. (See references of Elias and Cocroft for details). Geophones have been used in various arrangements to record substrate-borne vibrations in mammals for many years (A nice summary of the technical aspects of studying vibrational communication can be found in Wood and O'Connell-Rodwell 2010).

Molecular techniques create new research opportunities for studies of vibrational signals. The use of molecular techniques to determine what prey a spider has been eating is innovative and promises to be a new avenue of research for predator–prey relationships in spiders and insects. Paternity tests could be used to make the connection between reproductive fitness and courtship intensity. Is the spider or kangaroo rat that drums the most and at the greatest intensity really preferred by females and fathers the most offspring? The large number of insects, spiders and mammals that communicate by vibrations provides much opportunity for much future research. There is extensive opportunity, especially in insects and spiders, to conduct comparative research on vibrational communication in closely related species to tease out the pathways that evolution of the behavior might have taken (Cocroft et al. 2010; Elias et al. 2012). The use of molecular techniques promises to add a new and fruitful area of research in future studies.

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