

Possible Communication by Substrate Vibration in a Chameleon

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Plant-borne vibration is a common mode of communication among insects, but its use in reptiles has never previously been reported. One of us (KEB) observed that in response to human touch, veiled chameleons (*Chamaeleo calyptratus*) produce a distinct vibration which emanates from the body just anterior to the front legs. We made accelerometer recordings from plants on which chameleons were placed and determined that conspicuous vibratory signals were produced by males and females in response to human touch. When an adult male was placed on a plant with an adult female, it produced a variety of vibratory signals which varied in their gross-temporal and frequency characteristics. We hypothesize that these vibrations serve as vegetation-borne vibratory communication signals because (1) they were barely audible or inaudible to humans, whose auditory sensitivity exceeds that of chameleons but were easily detected by the accelerometer attached to a plant at 0.1 m distance and (2) they were produced in courtship and disturbance contexts in which one might expect communication to take place.

THE use of communication signals during courtship and other social interactions is a ubiquitous feature of animal social behavior. It is often possible for predators to use these signals to locate otherwise well-hidden prey (Cade, 1975; Ryan, 1985). In response, some animals have evolved “private” communication channels that are much more likely to be detected by the intended receiver than by any eavesdropping predator. One such adaptation is the use of vibratory signals that travel directly through vegetation. This mode of communication is widespread among insects (Michelsen et al., 1982; Henry, 1994). It takes advantage of the fact that the signal can easily be detected only by other individuals on nearby contiguous surfaces.

We have discovered an apparent example of the use of plant-borne vibratory signaling in a chameleon, which we believe is the first reported case of such behavior in any reptile. While handling a veiled chameleon (*Chamaeleo calyptratus*), one of us (KEB) noticed a buzzing sensation emanating from the body just anterior to the front legs. When the animal was held close to the ear, a faint, low-frequency sound could be detected. Suspecting that this might represent a form of substrate-vibration signaling, we made accelerometer recordings under a number of conditions that might be expected to elicit signaling behavior.

MATERIALS AND METHODS

On 14–15 April 1996, we recorded signals from three adult hand-reared individual *C. calyptratus* at an air temperature of 26 C. In each

case, one or more individuals was placed on a small branching shrub. An accelerometer (PCB U352B65, powered with a PCB U480E09 amplifier) was attached to one branch of the shrub with mounting wax, approximately 0.1 m from the position where the lizards were initially placed. The signal from the amplifier was recorded on a TEAC DA-P20 digital tape recorder with Apogee AD64 digital audio tape. Data were analyzed with Canary 2.0 software. During recording sessions, all behaviors were videotaped with a Nikon VN-959 camcorder.

RESULTS

In our first recording attempt, we placed an adult male on one branch of the shrub. In the absence of a second individual or any direct tactile stimulation by one of us, no vibratory signals were produced in a period of approximately 10 min. We then placed a receptive female on the same branch as the adult male. The male immediately changed its color pattern, flattened dorsoventrally, and approached the female in typical courtship behavior for this species (de Vosjoli and Ferguson, 1995). The male produced a series of vibrational signals which are described below. We detected no signals from the female.

We recorded a total of 137 signals from this male during a period of 66 min and quantified the salient features of 128 of these (11 signals were masked by incidental noise from the animals' movements). Signals were produced episodically in groups of 1–14, typically with a series of higher-pitched, shorter signals followed by one longer, low-pitched signal. The former

were associated with a slight tilting of the head, and the latter were associated with an obvious back- and-forth shaking of the head.

Signals of this male were variable in both their frequency characteristics and their gross-temporal features. The majority of these signals could be divided into two nonoverlapping groups based on their initial dominant frequency. Sixty-five percent (82/128) had a frequency of 105 Hz or higher. These calls were all short (mean length = 142 msec, SD = 49), relatively pure-tone sinusoidal signals without detectable frequency modulation (mean dominant frequency = 156 Hz, SD = 13; see Fig. 1A–B,D). Twenty-four percent (31/128) started with a dominant frequency below 90 Hz. These calls tended to be frequency modulated (mean dominant frequency = 49 Hz, SD = 20 at the start of the signal, mean dominant frequency = 25 Hz, SD = 12 at the end) and usually much longer than the calls of the first group (mean length = 948 msec, SD = 508; see Fig. 1A, latter part of trace). Occasionally we observed signals with features of both of the preceding groups: 12% (15/128) started with a frequency typical of the first group (mean frequency = 149 Hz, SD = 70), then dropped to a frequency typical of the second group (mean frequency = 50 Hz, SD = 27). These calls were usually intermediate in length (mean length = 730 msec, SD = 680 msec). All of these signals had a gradual onset and decay in intensity. None of these signals was audible to the human observers positioned approximately 1 m away.

We were also able to elicit calls by touching the animals lightly at the base of the tail. We recorded contact-elicited calls from the male ($n = 13$) and female ($n = 1$) described above and from another, younger male ($n = 8$). These signals from all three individuals were similar to the first call type described above: short (mean duration = 146 msec, SD = 60) sinusoidal signals (mean frequency = 152 Hz, SD = 29) with little or no frequency modulation (see Fig. 1C). These contact-elicited signals were faintly audible to us from a position immediately adjacent to the lizards.

DISCUSSION

We argue that the vibrations we recorded from these three individuals are designed to function as vegetation-transmitted vibratory signals. They are very unlikely to be auditory signals because they were either undetectable or barely detectable by our own ears, and the human auditory system is far more sensitive than that of the chameleon at all frequencies (Wever,

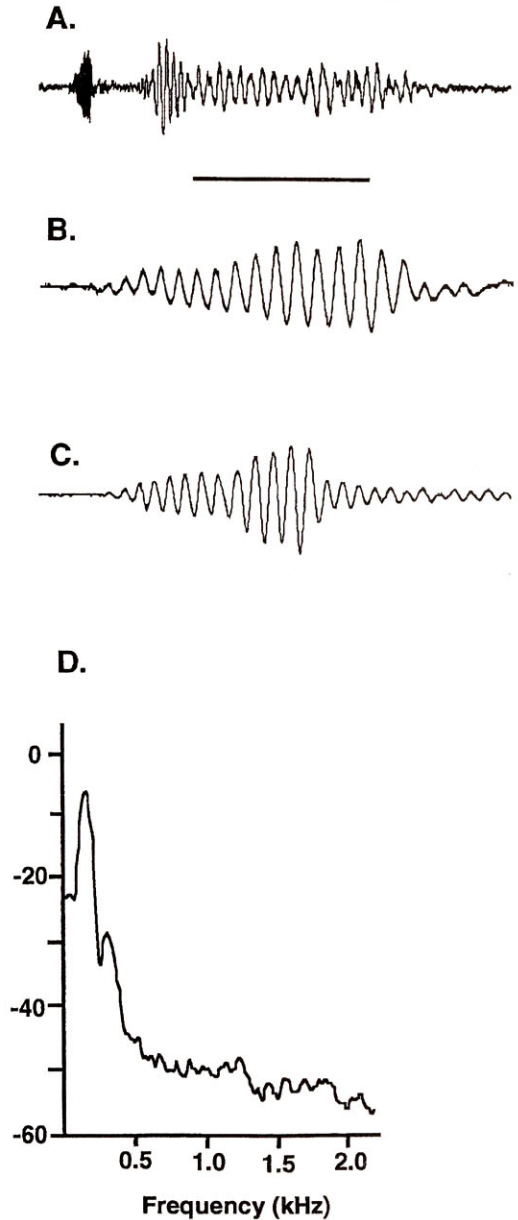


Fig. 1. Substrate-borne vibrational signals of *Chamaeleo calyptratus*. (A) Two signals from a courting male: the dominant frequency of the first is approximately 150 Hz, that of the second is 20 Hz. (B) Expanded waveform of the first signal shown in (A). (C) One signal from a female, elicited by contact. Scale bar represents 900 msec for (A), 60 msec for (B) and (C). The dominant frequency is approximately 165 Hz. (D) Amplitude spectrum (in dB) of the first signal shown in (A).

1968, 1969). On the other hand, they were easily recorded by the vibration-sensitive accelerometer a considerable distance from the source. We have no direct proof that these vibrations function in communication. However, the fact that they were produced only when a receptive female was presented to a male or when individuals were startled by direct touch, suggests that they serve a communication function. The variation we observed in signals of a courting male suggests the possibility of a repertoire of different signals (or possibly of a graded continuum, in which we observed primarily the endpoints). In any case, understanding the role of these vibrational signals in communication, and the importance of variation, will require not only additional observations of context-dependent signaling behavior but also an experimental investigation of the responses of potential receivers.

We are not aware of any published examples of communication through substrate vibration in reptiles. There are some examples of communication through ground-borne vibration in other vertebrates, including rodents (Rado et al., 1987) and frogs (Lewis and Narins, 1985; Cardoso and Heyer, 1995).

Sensitivity to ground-borne substrate vibration has been examined in a few reptilian species. Hetherington (1989) demonstrated that the sand-swimming lizard *Scincus scincus* can detect and orient toward vibrations from prey traveling through the sand. Hartline (1971) carried out a detailed study of the response to substrate vibration in a number of snake species. He identified two sensory mechanisms by which such vibrations could be detected: through direct stimulation of tactile receptors on the body surface, and through stimulation of the auditory system with the vibrations conducted through the head. The auditory mechanism was the most sensitive but was tuned to a fairly narrow range of frequencies from approximately 100–600 Hz, with peak sensitivity near 250 Hz. The tactile response system was less sensitive than the auditory system (in the range 200–500 Hz) but was much more broadly tuned with the greatest sensitivity occurring at 150 Hz and below. Hartline (1971) noted the superficial similarity of the auditory apparatus of snakes and chameleons and raised the possibility that the chameleon ear might also be designed for substrate vibration detection.

Wever (1968, 1969) studied the auditory sensitivity of four chameleon species. He noted that they are less sensitive to airborne sound than are most lizard families. In two of the species (*Chameleo senegalensis* and *C. quilensis*), he found

the greatest sensitivity in the range 200–600 Hz. These species appeared to have moderate sensitivity at 100 Hz (the lowest frequency measured). For *C. hohnelii* and *C. jacksoni* peak sensitivity occurred at much higher frequencies (1–10 KHz), and they had rather poor sensitivity to lower frequencies. He also stimulated each of these species with direct vibration of the head, and recorded auditory response. The results, in terms of frequency tuning and sensitivity, were very similar to those obtained with airborne sound. Wever's results may not be directly applicable to ours, because the same species were not examined and he delivered vibratory stimuli directly to the head, rather than through the legs and body as would be the mode of transmission for substrate-borne vibrations. Nevertheless, it appears possible from his results that, in at least some chameleon species, detection of low-frequency vibrations via transmission through the legs and body to the ear may be possible. It is also quite likely that these low-frequency vibration signals could be detected by tactile receptors in the legs or body.

There is circumstantial evidence to suggest that vibrational signaling may be quite widespread in the Chamaeleonidae. Vibration in response to direct touch has been reported in several species of the genus *Brookesia* (Raxworthy, 1991; Glaw and Vences, 1994) and *Rhampholeon* (Raxworthy, 1991). LeBerre (1995) states that female *Chameleo oweni* and *C. johnstoni* make low "purring sounds" in response to human touch or to the approach of a male. Parcher (1974) reports that courtship in some species of the genera *Chamaeleo* and *Furcifer* include head jerking movements. Because head twitching is associated with the production of vibratory signals in *C. calypratus*, it seems possible that there may be other species that also make use of vibratory signals.

Chameleons are highly adapted for arboreal life. They tend to be slow moving and cryptically colored to avoid being detected by predators. Communication through vegetation-transmitted vibration is a natural extension of these patterns of adaptation. Chameleons are famous for their use of visual signals in communication. It appears that, in at least one species, there may be another important mode of communication.

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