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Acoustic and Visual Display Behavior of Gekkonid Lizards

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SYNOPSIS. Visual and acoustic mechanisms of communication are compared. Their properties are found to be similar except that acoustic systems function more efficiently when light levels are low. The ability of geckos to receive and produce visual and acoustic messages is discussed. Geckos are found to have excellent vision and good hearing. They also possess the visual attributes and sound producing mechanisms necessary for complex displays. The display behavior of geckos is reviewed. Display types are categorized according to the display mechanism used. Visual displays are found to utilize color, pattern, posture, and movement. These displays are used in predator threat as well as in intraspecific social contexts such as aggression and courtship. Combined visual-acoustic displays involve color, pattern, postures, movement, and sound. Combined displays are used in predator threat and in intraspecific aggressive encounters. Acoustic displays have little or no visual component and involve sounds that may be single chirps or temporally patterned multiple chirps. The single chirps are associated with distress while the multiple chirp calls are heard in intraspecific social contexts. The displays of diurnal and nocturnal geckos are compared and it is found that differences are correlated with differences in their diel activity cycles. In conclusion, it is pointed out that many areas remain to be studied before gecko display behavior is well understood.

INTRODUCTION

The display behavior of geckos is a fascinating field of study for a number of reasons: gecko behavior is relatively unknown and numerous possibilities for study exist; within a single family are two very well developed types of display behavior; geckos are unique among the lizards in producing complex sounds that are involved in social behavior.

In this paper I will discuss the mechanisms of communication used by geckos, summarize their potential for message reception and production, review what is currently known about their display behavior, and compare gecko visual and acoustic display behavior.

MECHANISMS OF COMMUNICATION

Geckos have a variety of "choices" for channels of communication: chemical, visual, tactile, and acoustic. In this discussion I will restrict myself to the two mechanisms which have received most of the research attention: visual and acoustic.

The properties of visual and acoustic mechanisms of communication are largely similar; both systems provide animals with a rich variety of signals. Optical stimulus variables available are color, intensity or brightness, spatial pattern, postures, and movement. Acoustic stimuli are at least as diverse including pitch, intensity, frequency, and temporal pattern. Directionality can be a property of either system and with visual stimuli it is inherent in the system. Acoustic stimuli may be directional or not, depending on specific characteristics of the signal, and have the additional attribute of being able to go around corners. The strength of both systems is good, providing reasonable distance communication, but acoustic signals can be stronger and may be more efficient for long-distance communication. This is particularly true when ambient light levels are low. The amount of information conveyed is somewhat dependent upon how quickly

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one signal follows another. Acoustic systems have a very fast fade rate, while visual systems vary in their fade rates depending upon the stimulus variable being used. Thus, if postures or colors are used, fade is slow; but if movement is used, fade is fast. A visual display can be physically directed at a particular animal and can use stimuli appropriate to the receivers' sensory system. An acoustic display can be very specific for a receiving sensory system but acoustic signals are also frequently nonspecific and are heard by animals other than the intended receiver.

In summary, both mechanisms of communication allow the same types and richness of information to be conveyed over similar distances. The major difference is that acoustic systems function more efficiently when ambient light levels are low.

MESSAGE RECEPTION

Vision

Vision is a dominant sense in most lizards, and geckos are no exception. For many years the only general source concerning the reptile eye was a book by G. L. Walls (1942) but recently some additional work has been done and this is reviewed by Bellairs (1970) and Underwood (1970). I will briefly summarize some significant features of gecko visual reception.

The eyes of nocturnal animals are proportionally larger than those of diurnal animals, and nocturnal forms usually exhibit larger pupil and lens apertures. Geckos have prominent eyes and nocturnal members of the superfamily have larger eyes than their diurnal relatives (Werner, 1969). The retinas of most lizards are composed solely of cone cells that are sensitive to light and color. Most geckos have a retina of light sensitive rods and probably do not have color vision. The diurnal genera, such as *Gonatodes, Phelsuma,* and *Lygodactylus*, are known to have a cone retina that is, no doubt, a color receptor.

Visual acuity in lizards has not been well investigated and no work has been done with geckos. But some educated guesses can be made on morphology and behavior. The rod retinas of most geckos are probably very sensitive and provide good form vision. The diurnal geckos, also, no doubt, have good vision due to areas of concentrated cones or other means not yet well investigated. Behavioral observations clearly show that both diurnal and nocturnal geckos have excellent vision. I have observed captive geckos such as the diurnal *Phelsuma* orienting toward and approaching crickets at a distance of over 3 m. I have also watched the feeding behavior of small nocturnal geckos in the field. These animals *(Hemidactylus frenatus* Dumeril and Bibron) were seen to orient toward, and approach a mosquito landing approximately 3 m away. Individuals were also observed watching the flights of small insects which were quickly and directly approached when they landed. Many of these observations were made under low light intensities indicating further that geckos possess excellent visual acuity.

Hearing

Wever and his co-workers at Princeton have investigated hearing in lizards (Peterson, 1966; Wever and Hepp-Raymond, 1967; Wever and Werner, 1970). Wever has shown that a gecko ear is less sensitive than a typical mammalian ear but that within a restricted frequency range some species of geckos are as sensitive as many mammals. The range of sensitivity in geckos is from approximately 100 Hz to nearly 10,000 Hz and greatest sensitivity is in the 100 Hz-3,000 Hz range. Of the geckos studied, those with the most sensitive ears are *Coleonyx variegatus* Baird and species in the genus *Ptyodactylus*

MESSAGE PRODUCTION

Visual

The capabilities for producing visual messages are present in geckos. Striking patterns of blacks, browns, and whites are common. Vivid colors, from emerald greens to bright reds, blues, and yellows, are found in a number of species. In some, colors are combined into patterns giving additional display potential. Postures using body, tail, limbs, and head can also be used to produce a message. Movement is another potential source of message production. Head jerking, tail waving, strutting, and even push-ups have been observed. In addition, all of the above visual capabilities can, and frequently are, combined to produce a message.

Acoustic

Geckos have long been renowned among the lizards for their abilities to produce sounds (Smith, 1849; Evans, 1936; Mertens, 1946). Acoustic signals can be produced by the integument, such as in the genus *Teratoscincus* which makes a noise by rubbing caudal scales against one another. Geckos are apparently unique among the lizards in possessing vocal cords (Gans and Maderson, 1973) and this allows them to produce complicated vocalizations. Sounds range from barely audible squeaks and chirps to loud growling and barking noises. Many geckos have local names onomatopoeically derived from the sounds they make: *Hemidactylus frenatus* is called "chee chak"; *Gekko gecko* Lauranti is "tokay."

DISPLAY BEHAVIOR

Visual displays

For this discussion I have placed visual display in two contextual categories: threat or defensive—a display performed during a threat by a predator or during aggressive interactions with other geckos; courtship—a display performed to members of the opposite sex prior to copulation.

Defensive or threat displays are common in adult and juvenile geckos of both sexes. These are largely performed by nocturnal geckos and require proximity to stimulate the display. The simplest of these involve striking colors or patterns which when coupled with movement may function to startle or confuse a predator. Geckos in the genera *Eublepharis, Coleonyx, Gonatodes,* and *Sphaerodactylus* frequently have hatchlings and young animals which are more brightly colored or strikingly patterned than are the adults. *Coleonyx variegatus* use tail movements and specific postures in response to snake predators, and it has been suggested that this behavior results in directing attacks to the tail which is autonomized, allowing the animal to escape (Johnson and Brodie, 1974). I have observed *Eublepharis* (particularly juveniles) to respond to a human threat by vigorous tail waving and postures (Fig. 1).

Many threat displays do not involve color or striking patterns but do have strong postures and vigorous movements associated with them. Defensive displays in response to humans have been reported in the genera *Diplodactylus, Phyllurus, Gehyra, Heteronotia, Hemidactylus, Teratoscincus, Nephrurus, Gekko,* and others (Bustard, 1965, 1967; Mebs, 1966, 1973). These displays frequently make use of limb extension, back arching, inflation of the lungs, and tail waving. Some of these displays also involve limb extension and retraction, either a single motion (*Phyllurus*) or a continuous series of motions for several minutes (*Nephurus*). The above threat displays can be performed by males and females but are more common in males.

Threat displays are known to be used during intraspecific encounters as well as in a response to predators. I have observed *Gekko gecko* and *Teratoscincus scincus* Schlegel use similar visual threat displays to conspecifics as they use in response to human threats. It is not known if the other genera mentioned above use predator threat displays during intraspecific encounters but indirect evidence that they do can be derived from the discussion that follows.

Many geckos perform visual threat displays that are directed at conspecifics, but these have not been reported to be used in defense against a predator. Visual displays during aggressive encounters have been reported in the genera *Coleonyx, Lucasius, Hemidactylus, Lygodactylus,* and *Phelsuma* (Bustard, 1965; Greenberg, 1943; Greer, 1967; Marcellini, 1974), and I have ob-

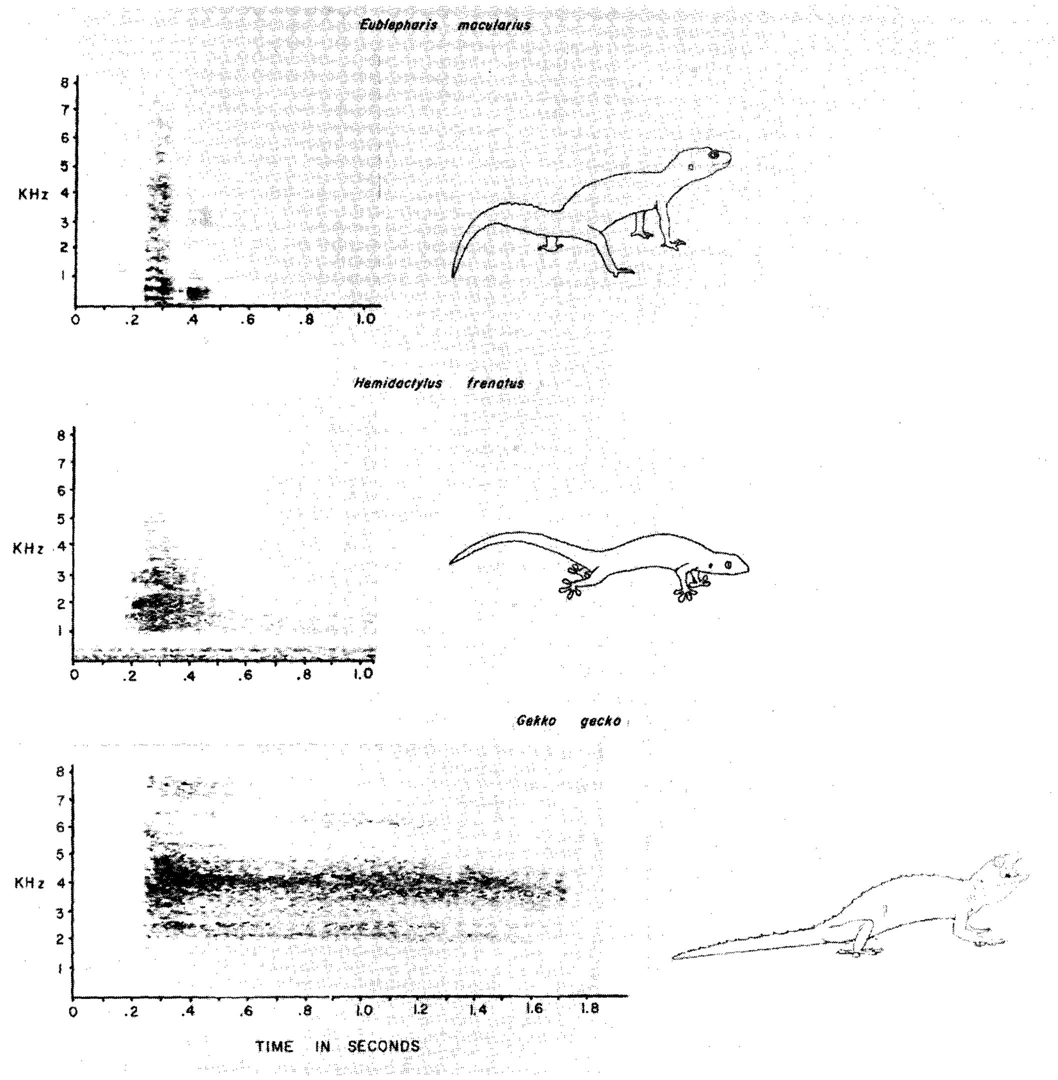

FIG. 1. Sonagrams of threat calls and drawings of threat postures for three species of gecko.

served visual threat displays in *Ptychozoon* and *Gonatodes*. These displays use posture, movement, color, and pattern.

The nocturnal genera *Coleonyx, Lucasius,* and *Hemidactylus* have very similar displays. These displays have only been reported to occur between males who are in close proximity. The body is arched and held high by the extended limbs while the head is usually held low. The geckos orient with their flanks parallel to each other and after some circling may attempt to bite their rival (Fig. 1).

The display of the nocturnal gecko *Ptychozoon lionatus* Boulenger differs from the above pattern in that the body is held low and the hind quarters are alternately raised and lowered. This is accompanied by the moving of the tail over the back at nearly right angles with the longitudinal axis of the body.

The diurnal genera *Gonatodes, Lygodactylus,* and *Phelsuma* have intraspecific threat displays that involve pattern, color, and movement to a greater degree than nocturnal genera (Greer, 1967; Kastle, 1964).

In a typical display the body is raised, the back is arched, the nose is pointed slightly down and the throat may be distended. The displays are given in a head-on or broadside position and the body positions may be changed as an animal moves closer to an antagonist. These postures are accompanied by side-to-side movements of the head.

In many diurnal geckos, colors are vivid and color differences between the sexes may exist. Postural attitudes are used by these geckos to better display colors and patterns. *Phelsuma* tilt their bodies toward an opponent showing their bright red or blue dorsal markings. *Lygodactylus* distends its throat exposing a black patch and inflates its abdomen showing a yellow midventral stripe.

The visual threat displays described for diurnal species of geckos differ from those of nocturnal species in that they can apparently be performed by both males and females (more commonly by males) and they do not require close proximity to elicit a display.

The similarity between threat displays directed at predators and those directed at conspecifics suggests that many of the genera above may be found to use their intraspecific displays in response to predator threat.

The function of visual threat displays directed at conspecifics is not known. The close range threats in nocturnal geckos may act to intimidate a rival prior to actual fighting. When given at a distance the threat displays of diurnal geckos may function in territoriality or spacing as has been suggested for visual displays of nongekkonid lizards (Carpenter, 1967).

Courtship displays

Courtship in geckos has only been described in a few species, but it appears that differences exist between diurnal and nocturnal animals. Greenberg (1943) described courtship copulation encounters in the nocturnal species *Coleonyx variegatus*. This animal demonstrates very little of what might be called display. The male approaches the female with head and body low and with tail waving. He may lick her briefly or merely pounce and bite finally securing a neck hold. I have similar observations on *Hemidactylus frenatus* and *H. turcicus* Laurenti.

The visual courtship displays of diurnal geckos are in marked contrast to those of nocturnal species. Displays are elaborate and involve postures, movement, pattern, and color. Courtship displays have been described for the genera *Phelsuma* and *Lygodactylus* (Kastle, 1964; Greer, 1967), and I have observed courtship in *Gonatodes*. The courtship displays appear nearly identical to the threat displays for these genera. The males begin to posture at a distance from the female of a few centimeters to up to 100 cm. Displays consist of raising the body, arching the back, distending the throat and posturing to expose color and patterns. Lateral head movements are also a part of the courtship display. If the female does not move off, the male will grasp the skin of her nape in his mouth and copulate. Females are largely passive but sometimes will actively solicit the male by approaching, nipping, and tail waving.

Visual courtship displays in geckos may function in the same manner as visual displays of other lizards. It has been suggested that male displays attract females and allow females to recognize males of their own species (Carpenter, 1967; Hunsaker, 1962).

Visual-acoustic displays

Visual displays may have acoustic accompaniments; they are also frequently produced alone. However, there are no reports of the acoustic portion alone; it is always heard coupled with a visual display.

Combined displays have only been observed in threat contexts either in response to a predator, or in aggressive interactions with another gecko. Males and females will produce threat sounds when approached by a predator but apparently only males vocalize during intraspecific aggressive encounters. Threat sounds in response to a human predator have been reported in the following genera: *Gekko, Diplodactylus, Lucasius, Nephrurus, Phyllurus*, and *Teratoscincus* (Bustard, 1965, 1967; Mebs, 1966; Wever *et al.*, 1963). In addition I have heard *Eublepharis macularis* Gray produce a threat call in response to a human. These sounds, all associated with visual displays, are produced at very close proximity to the predator; and are thought to startle it allowing the gecko time to escape. A typical threat sequence is described for *Nephrurus asper* Gunther (Bustard, 1967). This gecko postures, does push-ups, and when prodded lunges at its tormentor and utters rasping noise.

Threat sounds produced during intraspecific interactions have been reported in the genera *Phelsuma, Lygodactylus*, and *Hemidactylus* (Kastle, 1964; Marcellini, 1974). I have also observed *Gekko gecko* to use a threat call during intraspecific interactions. These calls are associated with the previously described visual displays and are produced when animals are in close proximity. They may function as a last minute intimidation or to startle an antagonist. A typical intraspecific threat is described for *H. frenatus* (Marcellini, 1974). Males posture vigorously from close to their opponents until one of the animals lunges at the other, opens his mouth and utters a rasping call.

Sonagrams of threat calls and associated postures for three species of geckos are shown in Figure 1. The calls for *Gekko* and *Eublepharis* are in response to a human predator while that of *Hemidactylus* was recorded during an intraspecific aggressive encounter. The vocalizations are all relatively short-duration single bursts of sound with a dominant frequency that varies from 1,000 Hz in *Eublepharis* to 4,000 Hz in *Gekko gecko*. All three sounds have harmonics that cover a reasonably wide frequency range. Intensity varies; the *Eublepharis* call is audible from only a few meters while *Gekko* is easily heard from over 20 m. The threat sounds of other geckos appear to have properties similar to these, although little quantitative data is available.

Acoustic displays

These displays are produced with little or no visual accompaniment. Two types of gecko vocalizations fall into this category: the single chirp or distress call and the multiple chirp call (Marcellini, 1974).

Single Chirp (SC): these vocalizations are the most commonly heard sounds produced by geckos. They have been reported for many genera and occur in both nocturnal and diurnal geckos (Frankenberg, 1975; Greenberg, 1943; Kastle, 1964). Single chirps are frequently produced by geckos when they are captured or handled. They also occur during interaction between individuals. Both sexes produce this call although males do so more frequently. In intraspecific interactions the call is produced when one animal bites or nudges another. In *Coleonyx*, Greenberg (1943) describes single chirps being produced when a male bites another male during aggressive encounters. I have reported a similar context for this call in *Hemidactylus frenatus* (Marcellini, 1974). I have also observed *H. turcicus* females to use this call while being bumped and licked by males.

Sonagrams of single chirp calls of *Hemidactylus frenatus* and *H. turcicus* are shown in Figure 2. The *H. frenatus* call was produced during handling of a male while the *H. turcicus* call was given by a female when bumped by a male. The *H. turcicus* single chirp is accompanied by a male multiple chirp call. These and other published sonagrams of single chirp calls indicate that the sounds are short and begin and end abruptly (Frankenberg, 1975; Marcellini, 1974). The calls cover a wide frequency range with dominant frequencies from 1000 Hz to 5000 Hz and harmonics to over 8000 Hz. Loudness varies: Some chirps can be heard only at distances under a few meters, while others are audible over 10 m away.

There are a number of speculations about the functions of the SC call. It might facilitate escape from a predator. The chirp expels air from the lungs making the lizard smaller; the sound might also startle the attacker. It has also been suggested

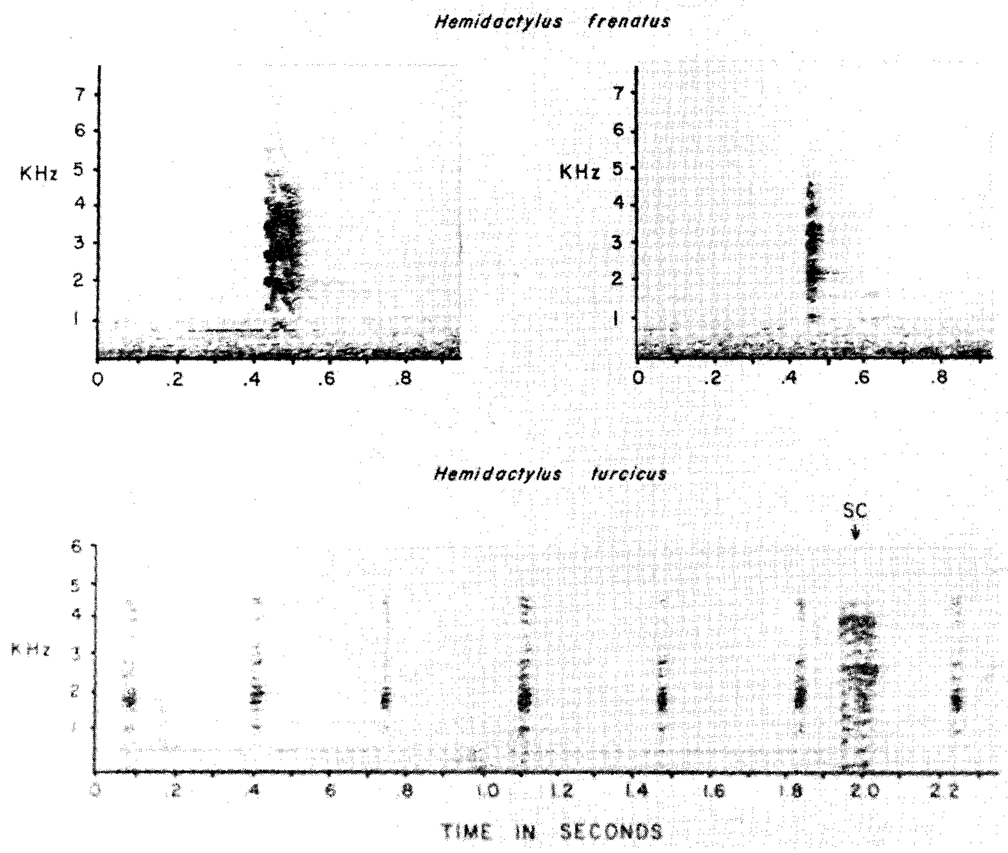

FIG. 2. Sonagrams of the single chirp calls of two species of gecko. The *Hemidactylus turcicus* SC call is accompanied by a multiple chirp call.

that the sound functions as a release call during intraspecific interactions. Frankenberg (1975) reported that a male *Ptyodactylus* released a hold on a female when she produced an SC call. But I have observed both male and female *Hemidactylus* to ignore single chirps produced by animals they held.

Multiple Chirp (MC): The multiple chirp call is a common vocalization that has been reported in a large number of genera (Brain, 1962; Evans, 1936; Loveridge, 1947; Mertens, 1955; Schmidt and Enger, 1957), but not in diurnal geckos. It can be produced by both males and females but is much more common in males. Multiple chirps are given in a variety of contexts but are more commonly heard during social interactions. Haacke (1969) states that calls are produced when animals emerge from diurnal retreats. Frankenberg (1974) mentions that geckos may call in response to another animal's call. Curry-Lindahl (1961) states that *Hemidactylus mabouia* Moreau de Johnes call upon seeing their mates. *Hemidactylus frenatus* uses multiple chirp calls in a variety of social situations (Marcellini, 1974). Males often produce the MC call when sighting an alien male at a distance. Aggressive encounters sometimes start with an exchange of calls and conclude with an MC call by the victor. In courtship copulation encounters males often utter the call prior to approaching the female.

Sonagrams of male MC calls of four species of geckos are shown in Figure 3. These plus published sonagrams for the genera *Ptyodactylus* (Frankenberg, 1974) and *Ptenopus* (Haacke, 1969) allow some

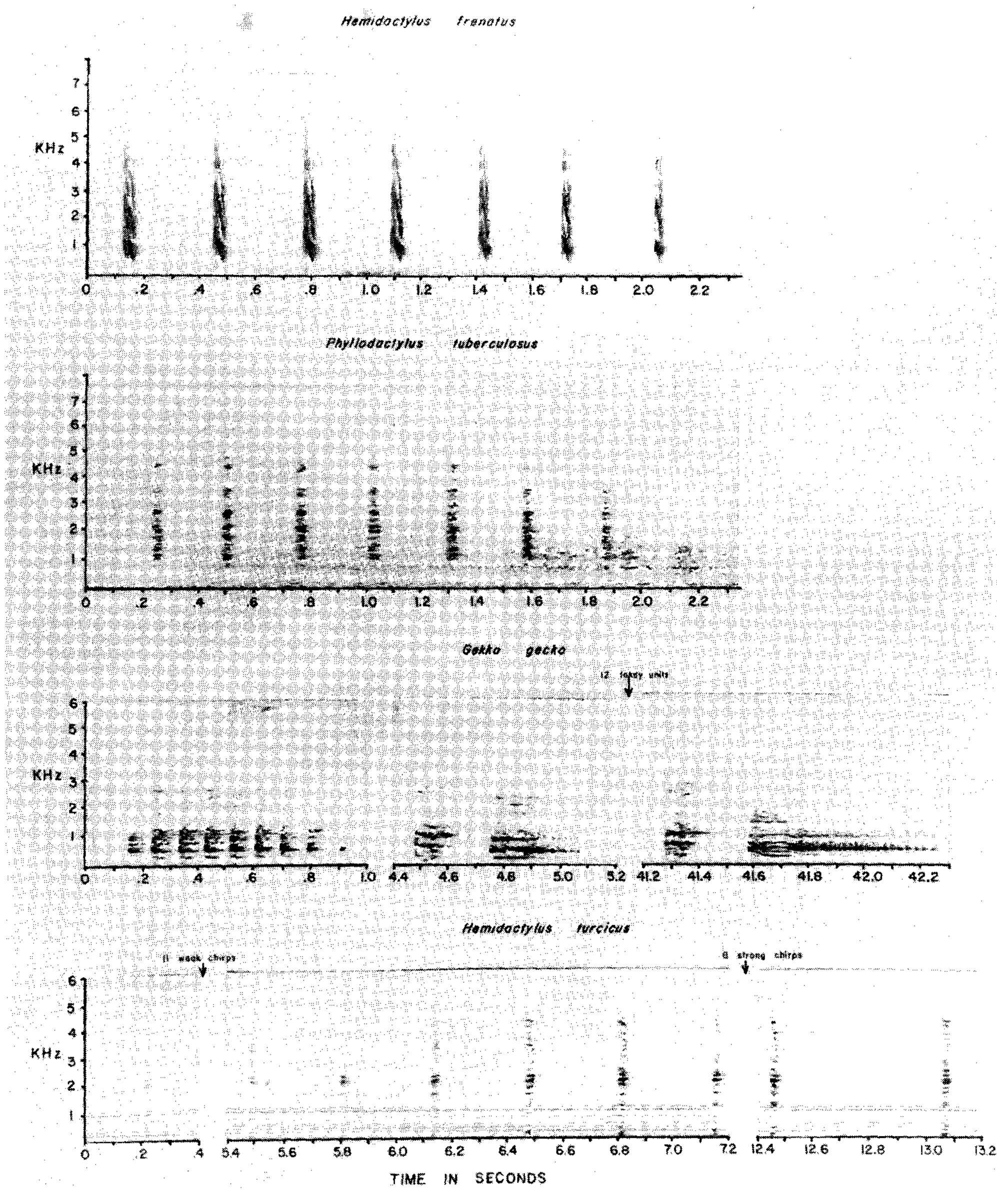

FIG. 3. Sonagrams of the multiple chirp calls of four species of gecko.

generalizations concerning call structure. The MC call consists of a series of chirps or barks that are produced in a temporal pattern. The dominant frequency varies from 500 Hz to 6000 Hz with harmonics to over 10,000 Hz.

Calls produced by an individual may vary in number of chirps but are uniform in structure. Frankenberg (1974) has reported change in call structure with context: male-male calls differ from male-female calls in being more protracted. Variation in MC calls between species has been mentioned by Haacke (1969) and Werner (1965). Species differences in duration of pauses and chirps, intensity pattern of chirps, and physical characteristics of the chirps are apparent in Figure 3. But, it would be premature to postulate taxon-specific calls on the basis of the limited information which now exists.

The variety of contexts reported for the MC call make functional interpretations difficult. Functional suggestions range from the attraction of insects (Beebe, 1944) to the more plausible possibility that the calls are important in social behavior (Wever *et al.*, 1963). They may play a part in territorial behavior (Mertens, 1946; Werner, 1965) and might act to attract females (Mertens, 1946). The fact that MC calls can also be produced by females makes the territoriality hypothesis more compelling.

I developed an experimental procedure to test the functional significance of the MC call of *Hemidactylus frenatus* (Marcellini, 1977). A male call was played to females and males in a choice situation. Females made no directed response to the call but males gave a significant negative response. Thus, it appears that a function of the MC call may be in spacing or territoriality.

COMPARISON OF THE DISPLAYS OF NOCTURNAL AND DIURNAL GECKOS

Table 1 shows a comparison of the display types of nocturnal and diurnal geckos. The similarities in the display behavior should not be surprising. The two groups have had a common ancestry; they have similarities in their population ecology and social systems. As a result they have the same messages to transmit. The few differences in display behavior are no doubt due to the differences in their activity cycles.

Visual and acoustic predator threats are not found in diurnal geckos. It would seem adaptive for a diurnal lizard to rely on spotting a predator at a distance and then rapidly seeking shelter rather than allowing a predator to approach closely before utilizing a threat display to stop the predator momentarily. A nocturnal gecko, however, has a greater chance of being surprised and thus needs to rely on a strong threat to stop a predator allowing the gecko to escape into the darkness.

The lack of a courtship display in nocturnal geckos may be due to differences in ambient light levels. In diurnal geckos the female can see the males and thus must be displayed at in order to keep her from escaping. In nocturnal geckos the male can approach closely without being clearly seen, rush the female and mate with her.

The multiple chirp call produced by nocturnal geckos appears to replace a part of the visual conspecific threat display of diurnal geckos. A visual threat at a distance would not normally be possible in nocturnal geckos because of low light intensities. An acoustic display would serve to declare an individual's presence from a distance thereby reducing territorial disputes and fighting.

CONCLUSION

The display behavior of gekkonid lizards has only relatively recently come under investigation and the study of their acoustic behavior is in its infancy. This review paper serves to point out many areas where work is badly needed. Additional species need to be studied particularly in the more primitive subfamilies. Quantitative descriptions of the displays are needed. This is especially true if we expect to determine if the displays are taxon-specific. The functions of many of the displays need to be clarified. This can be accomplished by additional contextual data but experiments must also be performed. The challenges are clear: We need only to apply ourselves.

TABLE 1. *Comparison of display types found in nocturnal and diurnal geckos.*

Display type	Diurnal	Nocturnal
Visual		
predator threat	no	yes
conspecific threat	yes	yes
courtship	yes	no
Visual and acoustic		
predator threat	no	yes
conspecific threat	yes	yes
Acoustic		
single chirp—distress call	yes	yes
multiple chirp call	no	yes

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