ACOUSTIC BEHAVIOR OF THE GEKKONID LIZARD, *HEMIDACTYLUS FRENATUS*

DALE L. MARCELLINI

ABSTRACT: The present study demonstrates that *Hemidactylus frenatus* has a vocal repertory of three functionally, physically distinct calls that are important in its social behavior. The multiple chirp (MC) call is the most common and is closely associated with agonistic behavior and territorial defense. The MC call has a consistent temporal pattern of chirps, and call rate varies directly with air temperature. Diel calling periodicity was investigated for the MC call and calls were observed to increase from dusk to a high in the early morning hours. Increasing call counts were positively correlated with numbers of active geckos. The churr call is infrequently heard, occurring only during aggressive encounters between ♂♂, and is thought to function as intimidation. The single chirp (SC) call is frequently heard and is closely associated with distress. The SC call may facilitate escape from predators. The acoustic behavior of *H. frenatus* is compared to that of other species of geckos and some correlates found.

MOST reptiles do not utilize sounds as intraspecific communication signals, but at least some members of the four major surviving orders have been reported to vocalize in social situations (Busnel, 1963). In most lizards sound production is lacking, or is limited to hissing, but a few can produce distinct vocalizations. The family Gekkonidae is noted for its vocal abilities which are thought to be of importance in intraspecific communication.

The significance of gecko sounds has been a source of controversy and speculation for years. Functional suggestions

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range from attraction of insects (Beebe, 1944) to the more plausible possibility that the calls function in social behavior (Brain, 1962; Evans, 1936; Mertens, 1955; Petzold, 1965; Wever et al., 1963a). Evans (1936) was one of the first to state that a species of gecko was able to make more than one type of sound, but until recently no description or analysis of gecko calls had been published. In 1969 Haacke described the calls of three species of South African geckos of the genus *Ptenopus,* and his paper remains as the only attempt to work quantitatively with gecko acoustic behavior.

The present paper describes the calls and documents some aspects of the acoustic behavior of *Hemidactylus frenatus.*

Methods

Data were gathered as part of an ethoecological study of a population of *H. frenatus* at the Hotel Valles in Ciudad Valles, San Luis Potosí, Mexico during March, April and May of 1969. Observations were made on marked animals of both sexes. Types of calls and the contexts within which they were given were noted. Five nights were chosen for hourly call counts and visual censuses of active geckos.

Vocalizations were recorded with a Uher 4000 Report-L tape recorder, having a frequency response of 40–20,000 Hz, a signal-to-noise ratio of 55 dB, and wow flutter ± 0.15% r.m.s. at 9.5 cm/s. A Sennheiser cardioid microphone with built-in wind screen and frequency response of 70–14,000 Hz was used in conjunction with a 61 cm diameter parabolic reflector. Graphic analysis of the calls was accomplished with a Kay model 7029 A sonagraph using a narrow band selector.

The method of recording was dictated by the habits of the geckos, and the type of call being recorded. Recordings were made of identified and unidentified free-living and captive individuals.

Results

Contextual observations and recordings of vocalizations demonstrated at least three functionally and physically distinct types of calls.

Multiple Chirp Call.—The most commonly heard vocalizations of *H. frenatus* were the multiple chirp (MC) calls. Over 300 of these calls were recorded during the 3-month study period. This call was given by adults of both sexes, but much more frequently by males. Aggressive males of a group were especially vocal, and most of the data and discussion are derived from MC calls of these animals. Geckos < 45 mm snout-vent length were not heard uttering the MC call.

Although MC calls were frequently produced it was extremely difficult to observe a calling animal. The geckos often called from dark secluded locations, and this, plus the short duration of the call, and the lack of associated vigorous body movements, made calling individuals difficult to locate. When observed it could be seen that animals called with their mouths nearly closed, and the only evidence that a call was being emitted was a slight rocking motion in time with the chirps of the call.

Context.—The contexts within which the MC call was given were varied. The call may be uttered by solitary animals with no apparent stimulus, or by both wild and captive animals within a group. After emergence from their diurnal retreats, geckos commonly called before moving to their feeding areas. These calls, that appeared to have no associated stimulus, might have been the result of an allelomimetic effect. Captive geckos could occasionally be stimulated to call by the playing of a recorded MC call near their cage. Free-living geckos also appeared to answer the calls of other geckos; however, this was impossible to verify due to the large numbers of calling animals.

The MC call was also commonly given at the conclusion of various activities. Three of 13 observed instances of eliminative behavior were followed by low intensity calls. The call was occasionally performed after successful feeding (15 of hundreds of feeding observations) and after many mat-

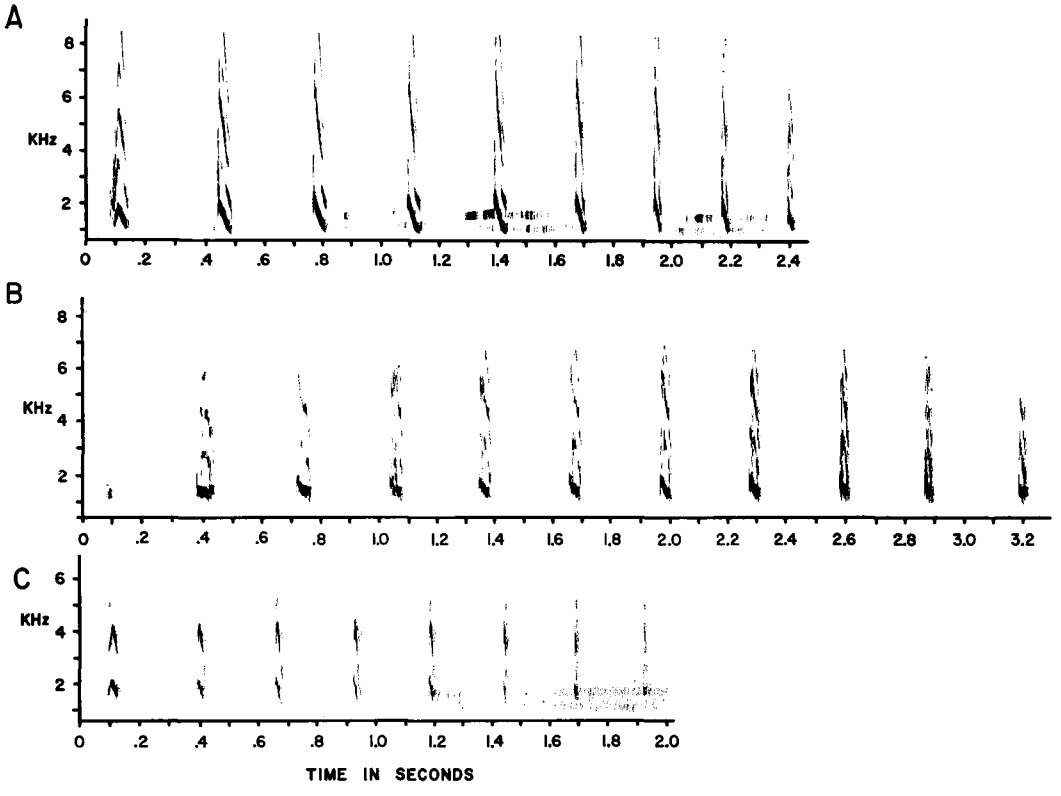

FIG. 1.—Sonagrams of the multiple chirp (MC) call of three adult ♂ *Hemidactylus frenatus* recorded in Ciudad Valles, San Luis Potosí, Mexico, March-May 1969. Fig. 1B is a recording of a captive animal and is completely free of background noise while Fig. 1A and C are sonagrams of calls of free-living geckos and show attendant background noise between the chirps.

ings (17 of 30). Nine of 10 observed male aggressive encounters were concluded with a MC call by the victor.

Males often emitted the MC call when sighting an alien male at a distance. The distance was highly variable, but a call was more likely as the distance decreased. The gecko at which the call was directed occasionally answered with a MC call. Calling between aggressive males was observed 25 times and was followed by aggressive encounters 10 times. In 8 of 30 courtship-copulation encounters, males uttered the MC call prior to approaching the female. On no occasion was a male observed to direct a MC call to a juvenile.

Females used the MC call with no apparent stimulus three times. One female was observed to utilize the MC call when approached by another female but numerous similar encounters produced no vocalizations. A captive female gave the MC call in response to a recorded male call on three occasions, but over 50 other females failed to respond to the same call.

Description.—The intensity (i.e., loudness) of the multiple chirp call was variable, and seemed to depend upon the context and level of excitement of the calling individual. The call given after elimination was of very low intensity and could barely be heard 2 m away. Other MC calls were frequently audible from 150 m distant. Calls directed at other males were always the loudest, being audible for more than 150 m.

The MC call is composed of a series of chirps, "gack-gack-gack", suggestive of the

barking of a small dog (Fig. 1). The dominant frequency of each chirp ranged from 1500 to nearly 2500 Hz, with harmonics at approximately 2000 Hz intervals above the dominant. Most of the sound energy was in the first two or three harmonics. In the first chirp of the call the dominant frequency rose from 1500 to 2000 Hz and then dropped back to 1500 Hz. In the subsequent chirps the pitch descended from 2000 to 1500 Hz. The frequency range was from below 1000 to over 8000 Hz, and further sonagraphic analysis showed harmonics that reached frequencies of over 14,000 Hz.

A statistical analysis of 143 MC calls was made. The mean number of chirps per call was 8.78 ± 0.15 (5–15). Call duration averaged 1.97 ± 0.04 (1.05–3.73) seconds while the call rate was 4.51 ± 0.06 (3.12–5.82) chirps per second. The variation in these three parameters was, no doubt, affected by the emotional state of the geckos but no quantitative data are available.

Duration and call rate varied in response to temperature. Fig. 1 shows two calls (A and B) recorded at approximately the same temperature (27 C). Call C has a greater number of chirps per unit-time, and parallel with this increase there is a reduction in duration of the chirps and pauses. Fig. 2 plots call rates against air temperatures at the time of the call. Air temperatures were taken from hygrothermograph records and give only an approximation of the temperature at the calling site of the lizard. In spite of this possible inaccuracy a highly significant ($P < .001$) positive correlation was found to exist between calling rate and temperature as determined by an F-test for regression.

Temporal Pattern.—The 54 clearest MC sonagrams were chosen, and individual chirps and pauses were graphically timed to the nearest 0.01 s and estimated to the nearest 0.001 s for the first seven chirp-pause units. The timings of chirps and pauses, and the sonagrams in Fig. 1, indicated that a temporal pattern existed in

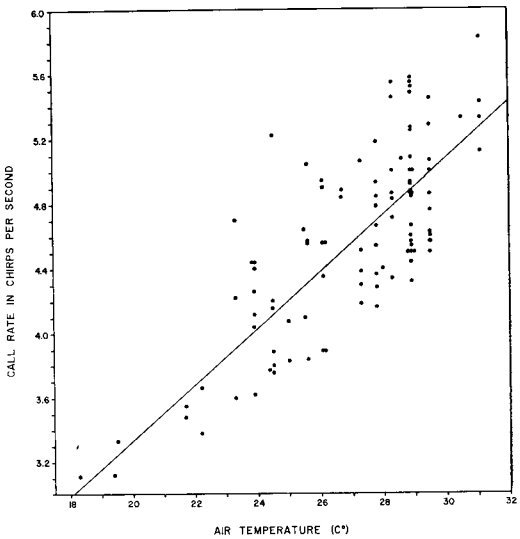

FIG. 2.—Relationship of rate of multiple chirp call (expressed in chirps per second) and air temperature with calculated regression line for 143 *Hemidactylus frenatus* calls recorded at Ciudad Valles, San Luis Potosí, Mexico, March-May 1969.

the MC call. The duration of each individual chirp and pause appears to shorten as the call progresses. To show this pattern, and to determine if other patterns existed, the timings of the chirps and pauses obtained for the 54 calls were expressed as a percentage of the total time for the seven units. Expressing the timings in this way reduced variation due to temperature effects mentioned previously.

Fig. 3 shows ranges, means, standard deviations and 95% confidence limits for each chirp and pause. The chirps and pauses shorten with each additional unit and, using the 95% confidence limits, it can be seen that a significant difference exists between the means of the early and late chirps of the call. The temporal pattern shown in Fig. 3 was consistent, and noticeable in all graphed MC calls.

Calling Periodicity.—Twenty-four hour calling periodicity was determined by hourly counts on 5 nights; 28 March, 8 and 21 April, and 1 and 21 May. Average hourly MC call counts and gecko counts

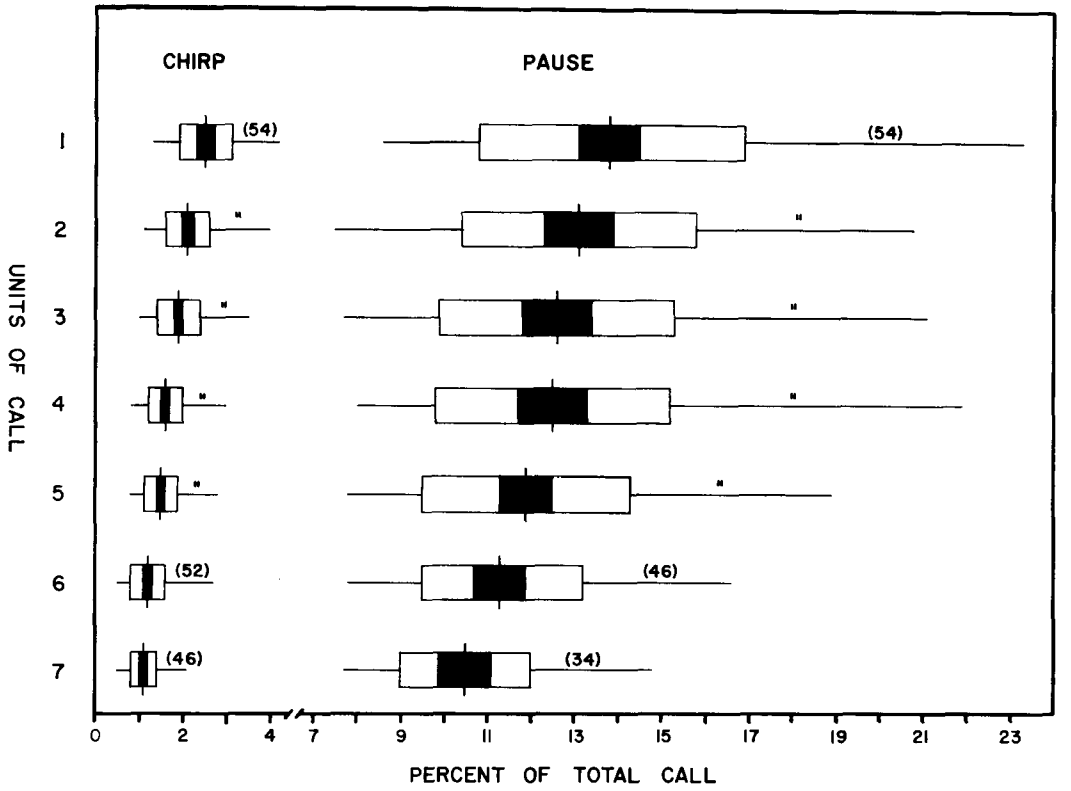

FIG. 3.—Duration of chirps and pauses of the multiple chirp call of *Hemidactylus frenatus* (expressed as a percent of total call) from Ciudad Valles, San Luis Potosí, Mexico, March-May 1969. Horizontal lines show observed ranges; rectangles mark standard deviation with solid black indicating 95% confidence intervals for the means. Mean values are indicated by vertical lines, and the number of records for each chirp and pause is shown in parentheses.

over a prescribed census route are plotted with hours of light intensity less than 10.76 lux in Fig. 4. Calls increased from an average of 19 per hour from 1800 to 1900 hours to a high of 89 per hour from 0300 to 0400 hours and then dropped to a low of 7 calls at dawn.

The average number of calls per hour is positively correlated with the average number of geckos censused. The difference between the number of calls and the number of geckos censused is due to all the audible calls being counted, while only the geckos in a confined area were censused. The limits of vocal activity are apparently determined by light intensity, with few calls occurring during daylight hours.

The close correlation between geckos censused and call counts breaks down for the period from 0200 to 0500 hours when calling apparently increases without a similar increase in gecko numbers. The reason for this incongruity is not known, but it is possibly related to the lack of human activity at this time. It was noticed that captive animals do not call if people are moving about in the vicinity of their cage, and free-living geckos in areas of low human activity seemed to call more than those in areas of high activity. Other factors such as wind and rain acted to decrease both gecko and call numbers.

Churr Call.—The churr call is an infrequently heard vocalization of *H. frenatus*.

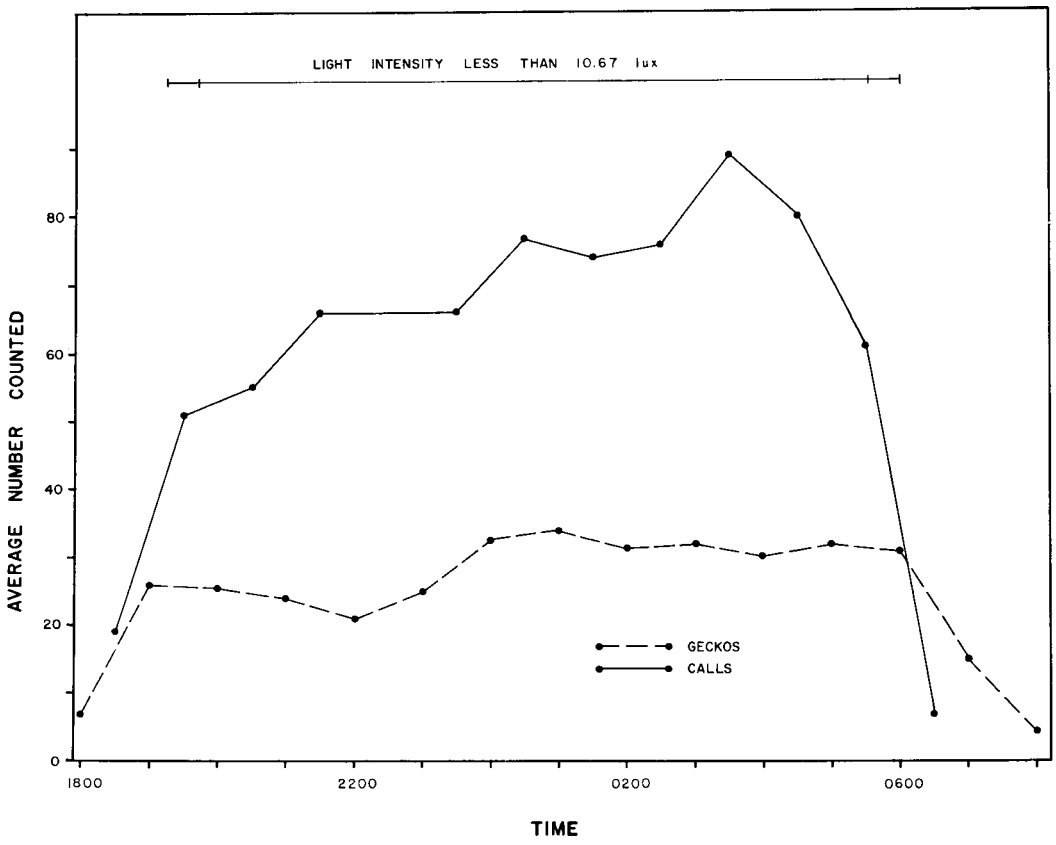

FIG. 4.—Mean number of multiple chirp calls of *Hemidactylus frenatus* per hour, mean hourly gecko census, and hours of light intensity less than 10.67 lux for five nights recorded at Ciudad Valles, San Luis Potosí, Mexico, March–May 1969. Vertical lines on light intensity line indicate variation in time of sunset and sunrise.

Twenty-three of these calls were heard during the 3-month study period, only 10 of which were produced by geckos under observation. The context of the churr call was highly specific. All 10 churrs were uttered by adult males during aggressive encounters. One of the antagonists (usually the resident) utilized this vocalization immediately prior to attacking the other animal. In all cases the animals were within one meter of each other, and were posturing vigorously previous to the production of the call. Often the call appeared to be completed while the male was lunging toward his adversary. The movements were very rapid and the call short, but it appeared that the mouth was kept open during the call. No females or juveniles (< 45mm snout-vent length) were observed to utilize this vocalization.

The churr is an extremely rapid series of short chirps similar in sound to the rattle of a high speed teletype machine. Fig. 5A shows sonagrams of this call for two males. These sonagrams are of the only two churr calls recorded, and both suffer from low intensity and background noise due to the distance between the calling animal and the microphone. In spite of the poor resolution, it appears that the call is composed of a series of extremely short sound pulses. The dominant frequency of the pulses is approximately 2000 Hz with harmonics at 1000 Hz intervals above the dominant. The

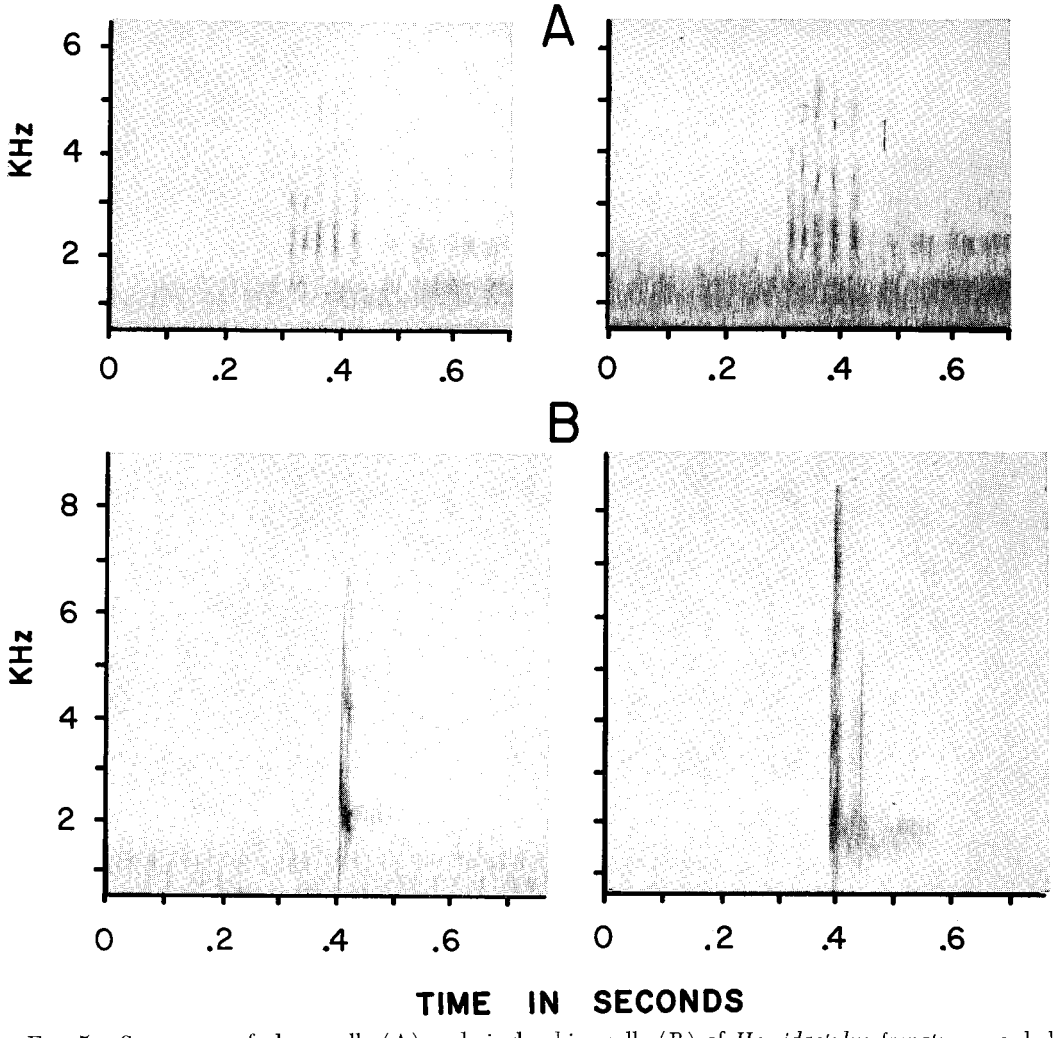

FIG. 5.—Sonagrams of churr calls (A) and single chirp calls (B) of *Hemidactylus frenatus* recorded at Ciudad Valles, San Luis Potosí, Mexico, March–May 1969.

duration of the two recorded calls is less than 0.2 s, and the other churrs heard appeared to be of similar duration. The loudness of the churrs was relatively constant and they were audible from approximately 35 m distant.

Single Chirp Call.—Hundreds of single chirp calls (SC) were heard while handling geckos, and from captive individuals, Also, on nine occasions free-living geckos under observation utilized this call. Both sexes produced the SC call although males did so more frequently. Adults, subadults and large juveniles utilized this call, but no animal < 35 mm snout-vent length was observed to utter the SC call.

Two contexts for the single chirp were observed. First, the call was often given when a gecko was initially grasped by a human, or during rough handling of a captive animal. Second, aggressive interactions between individual males also resulted in SC calls. When a large number of geckos were placed in a small cage a great deal of aggressive behavior ensued, and SC calls were produced. On nine oc-

casions SC calls were observed to follow aggressive encounters between free-living males. As the aggressor bit his victim, the bitten animal gave the SC call, struggled and invariably escaped.

The chirp is a single short pulse of sound ("gack") similar to the individual pulses of the multiple chirp call (Fig. 5B). The dominant frequency of the chirp is approximately 2000 Hz, with harmonics at 1000 Hz intervals above the dominant. Duration of the chirp is very short (< 0.05 s) and it begins and ends abruptly. The two chirps shown are of female (Fig. 5B, left) and male (Fig. 5B, right) calls in response to rough handling. Loudness of the SC call varies; some chirps can only be heard from a few meters away while others are clearly audible from 10 m. The level of intensity does not seem to be correlated with context, and the reasons for these variations are not known.

Discussion

Much more work must be done to elucidate the acoustic behavior of geckos before complete interspecific comparisons can be made, but some comparative discussion is possible.

Most of the calls mentioned in the literature are similar to the MC call of *H. frenatus* in structure and context (Beebe, 1944; Brain, 1962; Evans, 1936; Loveridge, 1947; Mertens, 1955; Petzold, 1965; Schmidt and Inger, 1957). The sonagrams of gecko calls in Haacke's (1969) work on three species of *Ptenopus* are similar to the sonagrams of *H. frenatus* in the present paper. *Ptenopus* calls also consist of a series of chirps, but they differ from the calls of *H. frenatus* in having a shorter call, and fewer chirps per call, as well as a narrower frequency range. Haacke suggests that these calls may function in territoriality and, or, to attract females.

A call similar in context to the churr call has been reported in tokay geckos (Wever et al., 1963b) and in *Nephrurus asper* (Bustard, 1967). These large geckos are belligerent, and when disturbed by a human or another gecko they open their mouths and utter a loud cry that is similar to the sound of a squeaky hinge. The call is frequently followed by a quick lunge at the intruder. In tokay geckos the call may be performed by both sexes, but much more frequently by males.

Vocalizations similar to the single chirp call are known to occur in *Cnemidophorus* (Wever et al., 1966) as well as in some geckos (Evans, 1936). In all cases these are short chirps or squeaks in response to handling and their functional significance is not known.

Functions for the calls of *H. frenatus* are suggested by the present paper and from the published observations above. The single chirp call is closely associated with distress, but its function in aiding the gecko is not known. The production of the chirp expels air from the lungs making the lizard slightly smaller, and the sound produced might act to startle a predator or aggressor. These two aspects of the call might aid the gecko to escape.

The churr call appears to be strictly a fighting call. It may function as a last moment warning or intimidation allowing the attacked animal to begin his retreat before bodily harm is inflicted.

The variable contexts within which the multiple chirp call is given make functional interpretations difficult. For the most part the call occurs when the animal is in an excited state, especially during social interactions. The extensive use of the call by males in apparent territorial disputes ties the MC call rather closely with agonistic behavior. The call appears to act as a warning to other male geckos to keep their distance. The call might also act as an attractant to females.

The effect of temperature on call rate in *H. frenatus* is not surprising in light of the many studies of animal sound production at varying temperatures. Call rates of insects (review by Frings and Frings, 1962) and of anuran amphibians (Blair, 1963) have been shown to increase with increasing temperature. Haacke (1969) also men-

tions that call rate in *Ptenopus* appears to drop with a decrease in temperature.

Reports of more than one type of vocalization in a gecko species have been scarce (Evans, 1936), and only Haacke (1969) has sonagraphic evidence for call differences. Two multiple chirp type calls were demonstrated by Haacke, differing in loudness and duration of various parts of the call, as well as in timing and frequency range of chirps, but no functional differences were observed.

Diel calling periodicity in nocturnal geckos has been mentioned by four authors. Brain (1962) states that *Ptenopus garrulus* calls in the late afternoon, with a maximum at sundown and the calls die away as darkness increases. Loveridge (1947), also working with *P. garrulus*, mentions that the vocalizations only occur during a brief interval at twilight. Evans (1936) studied *Gymnodactylus kotschyi* and found that calling frequency increased in the evening as the animals fed. Haacke (1969), in his work with *Ptenopus garrulus*, agrees with the above authors but also states that calling may continue throughout the night during rainy weather. Diel activity patterns of geckos have been shown to differ in differing environments (Marcellini, 1971). The geckos mentioned above have a very different habitat niche from that of *H. frenatus* and thus might be expected to differ in diel activity as well as calling periodicity.

This study begins to answer some of the questions concerning the acoustic behavior of *H. frenatus* but it also points out areas that require additional investigation. The functional interpretations for calls must be substantiated by experimental means. The consistent temporal pattern of gecko calls suggests that the vocalizations may be species specific, and the calls of other species need to be studied in detail so that comparisons can be made. Lastly, some thought should be given to possible functional homologies between the visual displays of diurnal lizards and the acoustic displays of geckos.

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Department of Biological Sciences, California State University, Hayward, California 94542