THE FUNCTION OF A VOCAL DISPLAY OF THE LIZARD
HEMIDACTYLUS FRENATUS (SAURIA: GEKKONIDAE)

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Abstract. An experimental procedure was devised to test the functional significance of the multiple chirp call (MC call) of Hemidactylus frenatus. The call was played to individual females and males in a choice situation. Females made no directed response to the male MC call, and seemed weakly stimulated to move. Males gave a significant negative response to the call and demonstrated more movement. The results of this study are compared to results of similar work with anuran amphibians and diurnal lizards.

The function of gecko sounds has been a source of speculation for years. Many early field observations suggest possible functions, but most statements remain unsupported by evidence. Functional suggestions range from attraction of insects (Beebe 1944) to statements that the calls are involved in social behaviour (Evans 1936; Mertens 1955; Brain 1962; Wever, Crowley & Peterson 1963; Petzold 1965; Haacke 1969; Frankenberg 1974). No experimental studies have explored the functional significance of gecko calls.

Hunsaker et al. (1968 unpublished manuscript) suggested that certain geckos cannot hear their own calls. Work on lizard sound reception by Peterson (1966), Wever & Hepp-Reymond (1967), Campbell (1969), and Wever & Werner (1970) and recent investigations concerning the sounds produced by geckos (Haacke 1969; Frankenberg 1974; Marcellini 1974), indicate that geckos of both sexes can probably hear their calls. Sensitivity curves for gecko ears determined by cochlear potentials show a maximum sensitivity from 100 Hz to 3000 Hz. Sonagrams of gecko calls show dominant frequencies within this range. Field observations further substantiate the hypothesis that geckos can hear their own calls. Geckos of both sexes will look at and orient toward calling individuals (personal observations).

Methods
The vocal repertoire of Hemidactylus frenatus has been determined to consist of three calls (Marcellini 1974). The churr call is relatively uncommon and occurs only at very close range in highly aggressive encounters between males. The single chirp call is heard during rough handling of an individual. The multiple chirp call (MC call) is the most common vocalization, occurring in a variety of social contexts, such as by both sexes (much more commonly males) when sighting another animal nearby; by males before and after copulations; and by males before and after aggressive encounters. In other gecko species a call resembling the MC call is also the most common call in social situations (Haacke 1969; Frankenberg 1974). For these reasons the MC call appears to hold the most potential as an experimental vocalization to determine call function.

A multiple chirp call produced by a solitary captive adult male H. frenatus was used in the experiments. The call was recorded in a small (30.5 x 30.5 x 46.0 cm) wire-mesh cage at an ambient temperature of 27.2°C, and was loud, clear and 1.9 s in duration. A 30-min experimental tape was made by duplicating the call at 1-min intervals.

The other taped sound used was white noise obtained by tuning an FM radio between stations and recording the resultant sound. This is a recognized method of obtaining a sound that contains all frequencies in nearly equal measure (H. Frings, personal communication). A 2-s segment of noise was duplicated at 1-min intervals to produce a 30-min experimental tape. Both tapes were recorded with a Uher 4000 Report-L tape recorder and a Sennheiser cardioid microphone.

Apparatus
A 3.66 x 0.61 x 0.61-m rectangular terrarium was constructed of an angle iron frame, glass panel front wall, sliding screen doors on top, masonite back wall, and 0.97-cm plywood ends. The floor was covered with 2.5 cm of fine sand, while the back and end walls were covered with a 1.3-cm thick polyfoam pad to reduce sound reflections.
The terrarium was lighted by two 25.4-cm black lights placed on top 91 cm from either end. Experimental animals were marked with orange radiant paint that fluoresces under black light. Observations were made from a blind placed directly in front of the terrarium.

Two 12.7-cm, 8-ohm high-compliance loudspeakers were mounted in the centre on the end walls of the terrarium, 2.5 cm from the top. The speakers were enclosed in 16.5-cm square boxes of 1.3-cm plywood and could be individually connected to a Uher 4000 Report-L tape recorder within the blind.

Experimental Animals

Twenty adult *H. frenatus* of each sex were obtained from a population at the Hotel Valles, Ciudad Valles, S.L.P., Mexico in August of 1969. Sexes were held separately; males were kept individually in small (20.0-cm high × 7.6-cm diameter) circular cardboard containers; females were maintained five to a cage in 30.5 × 30.5 × 46.0-cm wire-mesh cages. Mealworm larvae and water were provided ad libitum, and most of the animals remained vigorous. Deaths and escapes during the experimental period reduced the number of males to 18 and females to 15 at the conclusion of the month of experimentation.

Experimental Procedures

Tests were run at the University of Oklahoma Animal Behaviour Laboratory in October of 1969. Work began at dusk (20.30 hours) and continued until 22.00 or 23.00 hours daylight time. Air temperature during the experiments varied from 25 to 28°C. Experimental animals were placed under an opaque glass release jar in the centre back of the terrarium, and an experimental tape was played through the speakers for 5 min. Volume was adjusted to an intensity that approximated that of a call produced in nature and was kept constant in all experiments. The release jar was lifted by a string from inside the blind, and as the tape continued to play, the gecko was allowed 30 min to reach an end wall. Reaching an end wall constituted a choice, and the trial was terminated. If the animal did not reach an end wall within 30 min, the trial was scored no choice. A 30-min period was chosen because during trial runs many animals responded slowly. Animals were run consecutively for two trials, alternating the speakers used. Therefore, each animal had two trials, one from each speaker, in each experiment.

Three separate experiments were performed: first, the male multiple chirp tape was played to females; second, the male multiple chirp recording was played to males; and third, the white noise tape was played to males.

Results

The responses of female *H. frenatus* to a male multiple chirp call are shown in Table I. The combined results for both trials essentially produced a 1 : 1 ratio, strongly indicating that the choices of the females are at random. The upper portion of Table II shows the responses of male *H. frenatus* to the male MC call. The combined results produce a 2.4 : 1 ratio and are significant at the 2.5 per cent level.

According to the above data, male *H. frenatus* are repelled by a male MC call. To test the possibility that the geckos are avoiding the noise rather than the call a white noise of similar duration was played to the males. In both trials, and the combined trials, a ratio of approximately 1 : 1 was obtained (Table II).

Males and females also differed in numbers of animals making no choice. Fourteen of 37 females trials resulted in no choice, while only seven of 61 males made no choice.

| Table I. Responses of Female *Hemidactylus frenatus* to a Recorded Male MC Call |
|-----------------|-----------------|-----------------|-----------------|
| Trial | Toward | Away | No choice |
| 1     | 7      | 4    | 8    |
| 2     | 4      | 8    | 6    |
| 1 + 2 | 11     | 12   | 14   |

| Table II. Responses of Male *Hemidactylus frenatus* to a Recorded Male MC Call and to White Noise |
|-----------------|-----------------|-----------------|
| Experiment | Toward | Away | No choice |
| Male call: |
| Trial 1 | 4    | 12** | 2    |
| Trial 2 | 6    | 12   | 10   |
| 1 + 2 | 10   | 24** | 2    |
| White noise: |
| Trial 1 | 6    | 8    | 3    |
| Trial 2 | 6    | 7    | 2    |
| 1 + 2 | 12   | 15   | 5    |

*Significant deviation from expected; *P* < 0.05.

**Significant deviation from expected; *P* < 0.03.
The possibility that the lizard’s choices were being affected by some factor within the terrarium was tested by tallying the number of times the left and right ends were chosen. The right was chosen 47 times and the left 40 times. A chi-square value of 0.56 (df = 1, \( P = 0.45 \)) was obtained, indicating a non-significant deviation from a random distribution. Since an equal number of trials was made with each speaker, the geckos did not appear to demonstrate a preference for one end of the terrarium over the other.

Discussion
Females made no directed response to the male MC call, and in fact, seemed weakly stimulated to move. Results from experiments of this type with diurnal lizards and anuran amphibians suggested that the females would be attracted to the male call. Bogert’s (1947) recordings of the male call noted that female \textit{Bufo terrestris} were attracted. Martof & Thompson (1958) observed that recordings of breeding calls of \textit{Pseudacris nigrita} attracted gravid females. Awbrey (1965) tested several anurans in both choice and no-choice situations, and his results also indicate that breeding calls attract females. These authors point out that the call could function as an ethiological isolating mechanism between sympatric populations. In some species of diurnal lizards, females are attracted to male visual displays. Hunsaker (1962) observed that female \textit{Sceloporus torquatus} preferentially associated with models performing the display of their species. Jenssen (1970) demonstrated that female \textit{Anolis nebulosus} were attracted to a filmed species-specific display. Both authors suggest that the male display could serve as an ethological isolating mechanism in areas with closely related sympatric species.

In the present study there are at least three factors that might have contributed to the lack of female response to the male call. First, females cannot hear the male MC call. This is probably not true because, as discussed previously, hearing sensitivity and call dominant frequencies correspond. Second, the experimental call may not have been the proper stimulus for female attraction. Although the MC call appeared to be the most likely choice for experimentation, it is possible that another call, or some other factor, may function as a female attractant. Third, the physiological state of the females varied. (They were in different stages of the reproductive cycle with a few being gravid.) Physiological state is known to affect the behaviour of lizards (Ferguson 1966) and may be responsible for the inconclusive results for females in the present study.

Males generally gave a negative response to the male MC call. Further, their behaviour was not merely an avoidance of noise. Experimental studies with male anurans have shown that calls repel conspecific males. Duellman (1966) has described vocalizations of male dendrobatid frogs which keep other males away. Bogert (1947) noted that male toads were repelled by male breeding calls. Work with bullfrogs (Capranica 1968; Emlen 1968; Wiewandt 1969) has demonstrated that calls of males repulse other males, and that they are closely associated with the establishment and maintenance of territory. Studies dealing with male responses to displays in diurnal lizards have been few in number. Harris (1964) constructed a wooden model of \textit{Agama agama} which could be made to display by pulling a string. This simulated lizard elicited strong aggressive reactions from nearby males. Jenssen (1970) presented male \textit{Anolis nebulosus} with filmed displays and found that an aggressive response was produced. No choice experiments have been done to determine the response of male lizards to male displays.

The investigations above, and the present study, provide evidence that vocal displays of male geckos could function to establish and maintain territories. These territorial vocalizations tend to organize and space out the population and to limit the size of the breeding population. The vocalizations also reduce the chances for individual aggressive interactions by a distance warning system. This, in turn, conserves energy and lessens the chance for injury due to aggressive encounters. Males, for the most part, can maintain their territories merely by informing other males of their presence by a vocal display.

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References
Marcellini: Function of Gecko Vocalization


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