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ETHOECOLOGY OF *Hemidactylus frenatus* (SAURIA, GEKKONIDAE)
WITH EMPHASIS ON ACOUSTIC BEHAVIOR

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CHAPTER I

INTRODUCTION

Lizards of the family Gekkonidae have a widespread pantropic distribution, and in places where they occur are often the most abundant reptile. Houses seem to be a favorite habitat of some species of geckos and thus these animals can be conveniently observed. Within the family there is a vast array of structural and biological diversity. Geckos are unusual among the Sauria in that many species are nocturnal and are able to vocalize. These lizards are of particular importance to the study of the role of vocalization in social behavior since they have shifted from a diurnal to a nocturnal habit (Camp, 1923), and have acquired remarkable vocal abilities in the process. In spite of being abundant, obvious, and biologically interesting, the gekkonids remain a very large group of terrestrial vertebrates in which the ecology, and especially behavior, has not been studied in any detail.

In the present study the ethoecology of the Mexican house gecko Hemidactylus frenatus is investigated. Involved in this work is an analysis of the acoustic behavior and an experimental investigation of the functional aspects of gecko vocalizations.

CHAPTER II

TAXONOMY

The family Gekkonidae comprises a well circumscribed natural group of lizards with rather unstable internal taxonomic units. With the exception of the Gekkonidae (and possibly the Scincidae) all major families of lizards have proved to be fixed taxonomic units since the nineteenth century. Early efforts to classify geckos relied largely on the form of the digit (Boulenger, 1885). Recent attempts at classification have been based on the shape of the pupil (Underwood, 1954), and multiple external and internal characters (Kluge, 1967).

Underwood (1954) proposed that the Gekkonidae be divided into three families under the superfamily Gekkonoidea: Eublepharidae for geckos with true eyelids, Sphaerodactylidae for procoelous geckos with a spectacle, and Gekkonidae restricted to amphicoelous geckos with spectacles. Two subfamilies are proposed for the Gekkonidae: Diplodactylinae for gekkonids with straight vertical pupils and Gekkoninae for geckos with Gekko type pupils. This scheme has been demonstrated to be inadequate for delimiting natural assemblages of genera (Kluge, 1964; Stephenson, 1960).

The recent, widely accepted work by Kluge (1967), utilizing 18 diagnostic characters, groups the genera into four subfamilies: Eublepharinae, Sphaerodactylinae, Diplodactylinae, and Gekkoninae. Kluge (ibid) also proposes a phylogenetic relationship for the subfamilies. The order from primitive to advanced is Eublepharinae, Diplodactylinae, Gekkoninae, and Sphaerodactylinae.

Lower taxons within the family Gekkonidae are rather stable, with most genera being easily recognizable groups. The major taxonomic difficulties in the family are in phylogenetic relationships between genera and in relationships between Old and New World species and subspecies (Dixon, 1964; Kluge, 1969; Underwood, 1954).

The higher taxonomic categories and evolution of gekkonid lizards seems to have been resolved by Kluge and his classification will be followed in this paper.

Wermuth's (1965) checklist of the Gekkonidae of the world lists 83 genera, 673 nominal species, and 172 subspecies. The genus Hemidactylus is the largest, and accounts for approximately 10 per cent of the total number of species (76 species, 13 subspecies), excluding Gymnodactylus and Phyllodactylus which are thought to be polyphyletic (Kluge, 1969).

CHAPTER III

DISTRIBUTION AND DISPERSAL

Distribution

The family Gekkonidae is found on the majority of land masses between latitude 50° N and latitude 50° S. It appears that southeastern Asia, in the late Mesozoic, was the region and time of origin and early evolution of the family (Kluge, 1967). From this region the Eublepharinae have become circumglobal with major centers of evolution in the New World and in Africa. The relatively primitive Diplodactylinae are restricted to the Australian region, while the Sphaerodactylinae are restricted to the New World. The Gekkoninae evolved and dispersed westward through southwestern Asia to Africa and Madagascar. This subfamily is also present in the New World and on many of the Pacific islands. (Darlington, 1957)

The genus Hemidactylus has wide geographical distribution, being found in nearly all the major land masses and many islands. The major center for speciation has been Africa, with south-central Asia the secondary center (Kluge, 1964). Approximately 70 per cent of the Old World species and subspecies of Hemidactylus are found in central and northeastern Africa. Central and southern India, including Ceylon, have approximately 29 per cent of all Old World species and subspecies.

Most species of Hemidactylus have relatively small geographic ranges, however some exhibit extremely wide ranges. The species with great vagility and ecological plasticity are often aptly referred to as "weedy" species. The common half-toe gecko, Hemidactylus frenatus, is one of these "weedy" species and is pan-tropical in distribution. From its origin in southeast Asia it has spread to the East Indies, Africa, Australia, the islands of the mid-Pacific, and to Mexico (Kluge, 1967; Schmidt and Inger 1957; Underwood, 1954).

Published records from Mexico have been exclusively from states on the Pacific slope. Smith and Taylor (1950) only mention localities in the state of Guerrero in the region about Acapulco. Liner and Dundee (1969) extend the range southward with a locality record in Oaxaca. The Natural History Museum at the University of Kansas has records from the states of Guerrero, Oaxaca, and Chiapas. Inquiries to the University of California Vertebrate Museum and the American Museum of Natural History list only localities in these three states. Only two eastern slope collection localities have been found. A hatchling specimen of H. frenatus in the collection of Texas A & M University was taken three miles northeast of Tamazunchale, San

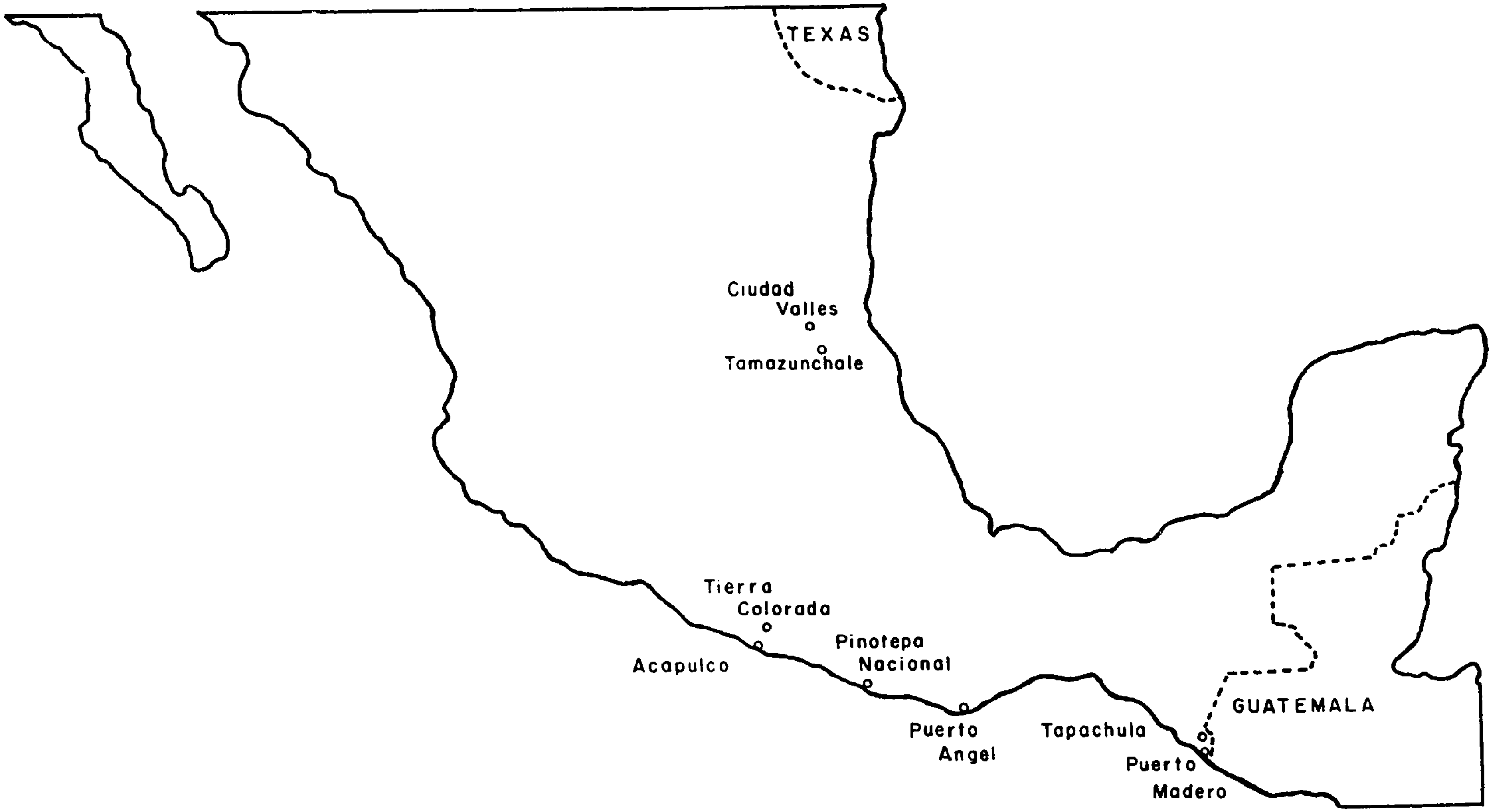
Luis Potosí, 30 December 1951 (James R. Dixon, personal communication). The National Museum in Washington, D.C. lists a record from Ciudad Valles, 29 December 1965. Fig. 1 shows Mexican collecting localities for *H. frenatus*.

Dispersal

The widespread distribution of geckos and their presence on islands far from major land masses brings up the question of dispersal routes. In their movements from the Old to the New World geckos have apparently utilized two major non-human assisted dispersal routes. The first was the Bering land bridge during the Cenozoic (Repenning, 1967). It is thought that the progenitor of the New World Eublepharine came by this route (Kluge. 1962). The second was by fortuitous trans-oceanic dispersal. The gekkonine genus *Tarentola* has been cited by Kluge (1967) as an example.

As a group, geckos seem to have a high probability for over-water dispersal for a terrestrial vertebrate (Simpson, 1952). The following characteristics, outlined by Kluge (1969), support the idea that geckos can sustain long over-water movements: (1) small adult size, (2) adept at clinging to moving structures, (3) insectivorous nature, but can ingest plant exudate, (4) retain sperm, (5) withstand long periods without food or water, (6) impervious skin to water loss and uptake of salts, (7) secretive, found in cracks and crevices and under bark, (8) gregarious, (9) high population densities, (10) broad habitat preference, (11) communal egg

Fig. 1. Locality records for *Hemidactylus frenatus* in Mexico.



laying, (12) calcareous egg shell, (13) adhesive eggs, (14) eggs withstand long periods of exposure to sea water, (15) early sexual maturity.

Geckos have also been aided in their movements by humans. The method of dispersal of Hemidactylus frenatus was probably by this means. These animals were, no doubt, brought to the New World on ships across the Pacific and possibly on more than one occasion. The evidence for such a hypothesis is as follows: (1) they do not appear to differ from the Old World forms (Kluge, 1969; Loveridge, 1947; Smith and Taylor, 1950), (2) their New World geographic distribution is almost entirely within human settlements, especially in ports and along routes of commerce, (3) most New World locality records are on or near coasts and they do not form a continous geographic range, and (4) the dates of introduction have been relatively accurately established (Kluge, 1969). Human aided dispersal assures that this cosmopolitan gecko will further extend its range in the New World.

CHAPTER IV

ETHOECOLOGY

Introduction

Studies of natural populations of geckos in the genus *Hemidactylus* are rare and have been largely restricted to the Old World (Cagle, 1946a; Church, 1962; Church and Chun-Sim, 1961; Mahendra, 1936). New World hemidactylids have been the subject of a few short ecological papers (King, 1959; Rose and Barbour, 1968) and a relatively large number of taxonomy and distribution papers.

This study is the first ethoecological work done on *Hemidactylus frenatus* and the first detailed investigation of any member of the genus in the New World. Data gained from this work will be compared with other investigations of lizard ecology and behavior, and particularly with data from other members of the family Gekkonidae.

Description of Species

World

1836 *Hemidactylus frenatus* Schlegel, in Dumeril and Bibron, *Erpetologie generale* 3: 366-368.

Mexico

1939 Hemidactylus frenatus Taylor, Univ. Kansas Sci. Bull., 26: 444.

Type Leyden Museum

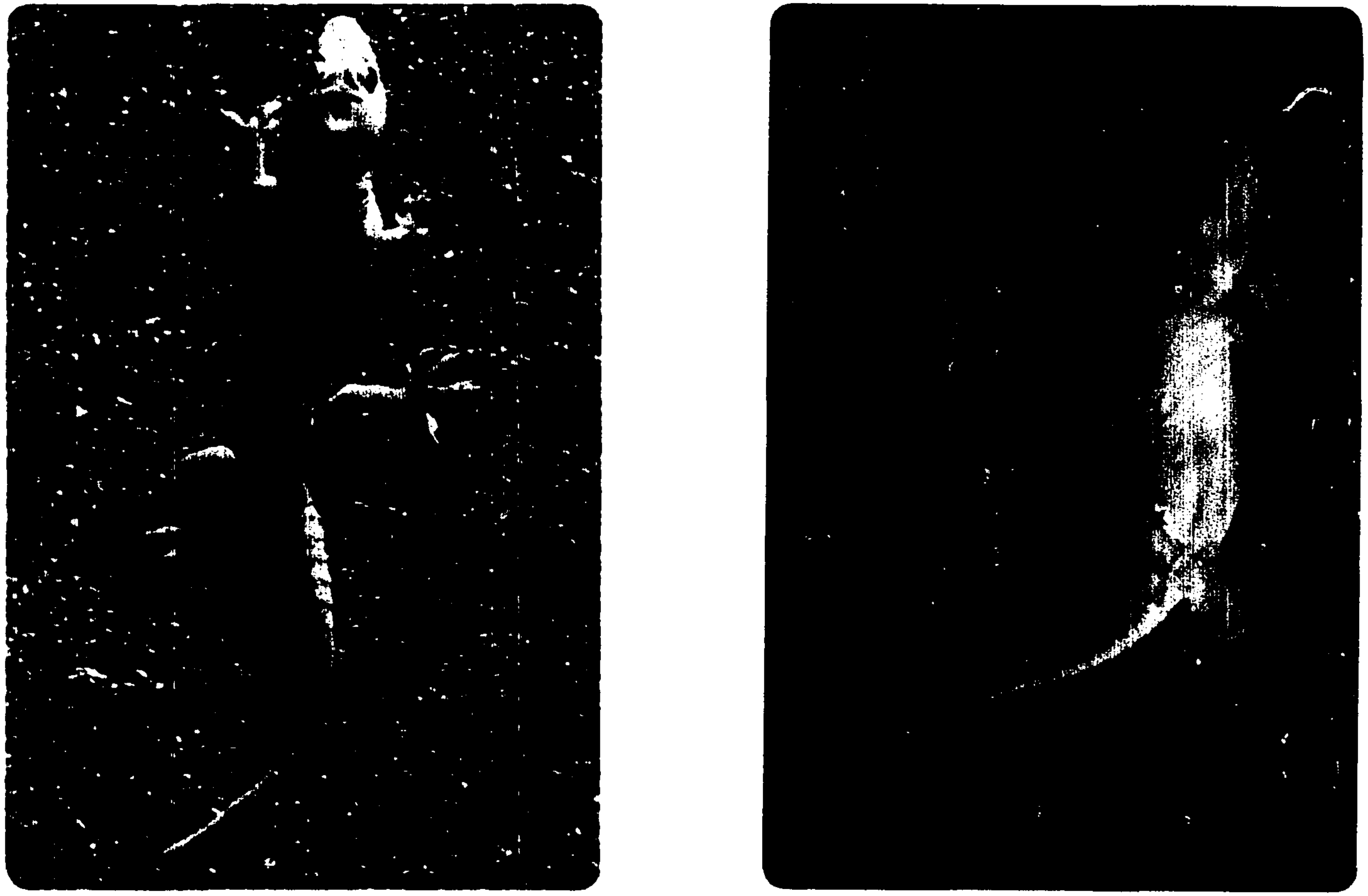
Type Locality Java

Hemidactylus frenatus can be separated from other members of the genus in Mexico by the following morphological features given in Smith and Taylor (1950).

> Small granules on the dorsal surface with only a few relatively small convex tubercles, these usually on posterior part of body; femoral pores 15-18 on each side not separated mesially.

The color in life varies from a light uniform flesh color to blackish above, either uniform or with a distinct pattern showing spots and distinct laterodorsal lines. The underpart of the body varies from nearly white to canary yellow. The dorsal color changes seem to depend somewhat on light and environment. At night in artificial light they are nearly flesh color when on white walls and rather grayish on darker substrates. Specimens taken in daylight are usually much darker and with more prominent dorsal patterns of lines. The sexes are similar in body form and color. Hatchlings and juveniles are similar in coloration to adults but with more conspicuous dorsal markings. Fig. 2 shows dorsal and ventral views of a male H. frenatus.

Fig. 2. Dorsal and ventral views of adult male *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico.



Description of Region and Study Area

Physiography

The study area was located in the town of Ciudad Valles, San Luis Potosí, Mexico, near the southern border of the state of Tamaulipus on the verge of the eastern coastal plain of Mexico. To the west, the Sierra Madre Oriental rises abruptly to an altitude of nearly 1800 m, to the east, a single anticline separates the town (altitude 91 m) from the coastal plain. Rivers, arising in the Sierra, run down deep east-west oriented canyons and emerge into the valley containing the city. These mountain torrents combine into a few relatively large rivers, such as the Río Panuco, which drain into the Gulf of Mexico.

Climate

The region around C. Valles is essentially tropical in climate, being below the tropic of Cancer and at an altitude of only 91 m. The mean annual air temperature is from 20 to 25 C while relatively high diurnal temperatures (29-32 C) contrast with cool nights (20-24 C) (Vivo-Escoto, 1964: 199). The daily range of temperature often exceeds the mean annual range by many degrees. The highest temperatures in the area occur in June, July and August and can reach 40 C. Lowest temperatures are found in the months of December, January and February. In these months polar outbreaks can occur which produce "Nortes" (Northers) which sweep down the Gulf coast. Typically the "Norte" brings cold dry air, heavy winds, cloudy skies, and occasional squalls. In 1951 an unusually severe outburst occurred in February and produced killing frosts in the northeastern Gulf coast region of Mexico (Miller and Gould, 1951). Although rare events these "Nortes" probably play an important role in limiting the northward spread of the tropical biota of eastern Mexico.

The C. Valles region sustains an annual rainfall of between 1000 to 1400 mm (Mills and Hull, 1949). Most of this is due to easterlies or trade winds which sweep over the warm surface of the Caribbean and the Gulf of Mexico absorbing vast quantities of water. As these trade winds are forced to rise and cool along the high windward-facing slopes of the Sierra Madre Oriental they release their water vapor as rain. Maximum rainfall occurs in the months of June, July, August, and September, but some rain falls in every month (Vivo-Escoto, 1964: 203). Relative humidity in the area is consistently high, averaging over 70 per cent much of the year. It varies from an average of 60 to 70 per cent in March to 80 per cent and above in the rainy season (Vivo-Escoto, 1964: 200).

A hygrothermograph was used to record daily temperature and humidity changes during the three months of this study (March, April and May). Table 1 shows a summary of these data plus the number of days of precipitation. These data demonstrate the rather stable temperature and humidity

Table 1. Weekly temperature, relative humidity and precipitation data for study area March 1 to May 31, 1969 excluding week of May 10 (hygrothermograph data).

	Temperature					Relative Humidity			Precipitation
Week	Absolute High	Average High	Absolute Low	Average Low	Average	Average High	Average Low	Average	Number of Days
3/1-3/8	32.2	25.4	13.0	14.5	20.0	99.5	58.2	78.8	2
3/9-3/15	29.4	24.9	12.8	15.5	20.2	94.1	53.7	73.9	1
3/16-3/22	29.5	26.6	10.5	16.0	21.3	94.4	46.4	70.4	1
3/23-3/29	33.9	28.6	16.6	19.9	24.3	100.0	29.3	74.7	1
3/30-4/5	32.3	29.2	18.3	20.6	24.9	96.1	53.0	74.6	2
4/6-4/12	33.4	30.3	20.6	23.3	26.8	99.9	65.1	82.5	1
4/13-4/19	35.6	32.3	21.1	24.6	28.5	96.7	45.4	71.1	0
4/20-4/26	30.5	29.9	22.2	23.0	26.5	93.3	58.6	76.0	0
4/27-5/3	36.1	29.7	22.7	23.4	26.6	99.9	61.1	80.5	4
5/4-5/10	36.7	33.0	23.3	25.3	29.2	98.8	56.0	77.4	0
5/18-5/24	32.3	32.6	23.9	24.5	28.6	97.6	50.8	74.2	0
5/25-5/31	32.3	32.3	22.7	24.2	28.3	97.5	53.7	75.6	0

regimes during the study period. Average temperature varied only 9.2 C and average relative humidity only 12.1 per cent. The precipitation listed in Table 1 was of two types. The first, and most common, was a light drizzle that generally occurred at night. The second type was thunder storms which usually struck in the evening and were often quite strong. A light morning dew was also common, especially in March and April.

The winds around C. Valles are generally out of the east and can be quite strong, but the protected location of the town results in only moderate winds, except during storms. Hurricanes, which originate in the Caribbean Sea, can occasionally reach the coast of Tamaulipus and have been known to cause damage in C. Valles.

Fig. 3 shows two reproductions of 24 hour hygrothermograph records. The pattern of daily temperature and humidity changes seen on these two days are representative of the extremes for the three month study period. March 5-6 was a cool day early in the study, while May 7-8 was a warm day near the end of the study period. Temperatures tended to be highest in the early afternoon and lowest in the early morning hours with no abrupt changes. Relative humidity, of course, reflected the temperature changes and was highest at night and lowest during the afternoon. Changes in humidity were also rather gradual, occurring over two and three hour periods.

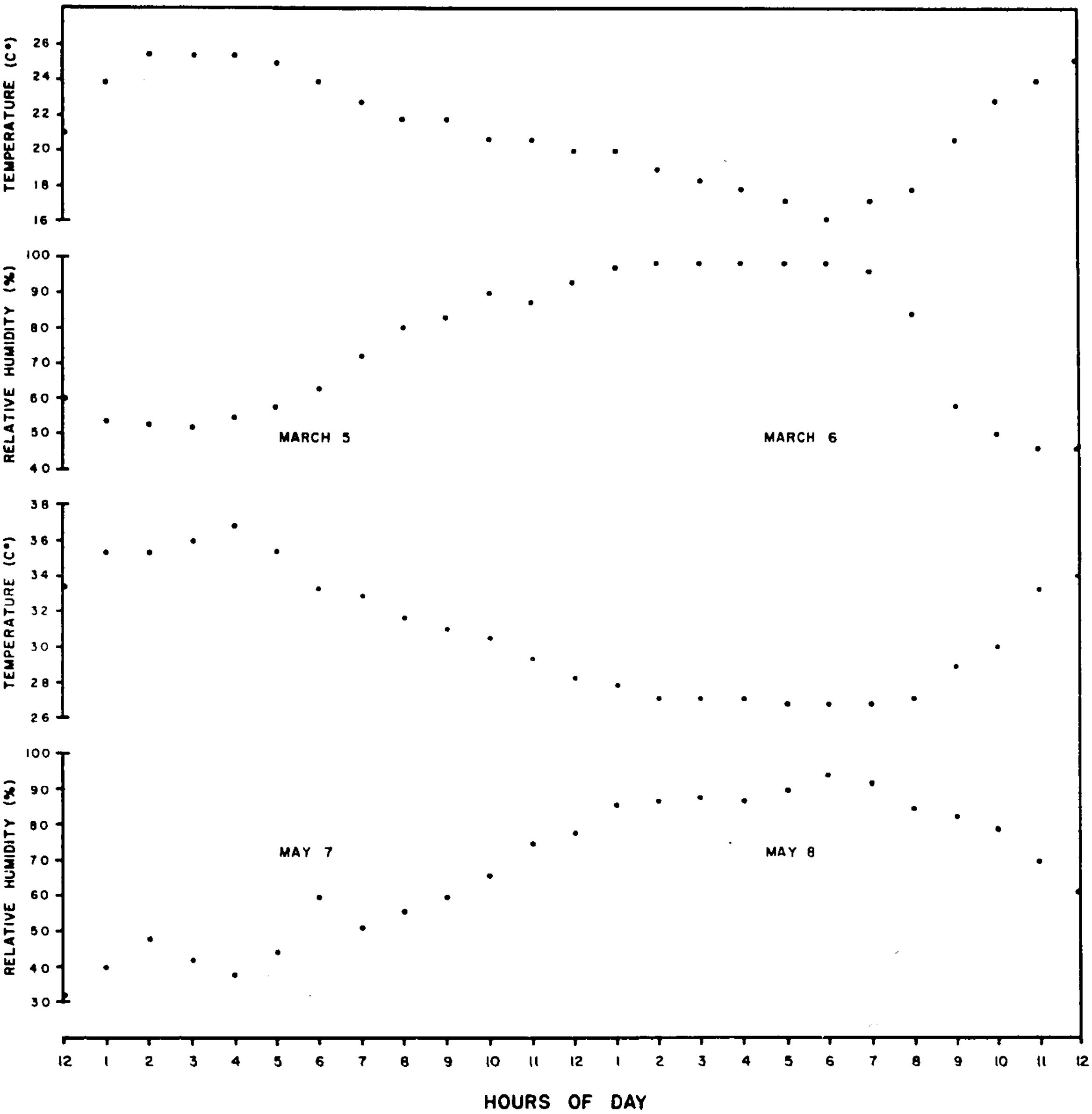


Fig. 3. Temperature and relative humidity records for two 24 hour periods (March 5-6 and May 7-8) from Ciudad Valles, S.L.P., Mexico, 1969.

Vegetation

In Mexico, *H. frenatus* is not generally associated with regional vegetation, and only slightly with cultivated plants. Vegetation, however, may be important as an indicator of suitable climatological regions for the species. It is also possible that *H. frenatus* will colonize areas other than human habitations, as the species has done to a limited extent in the Old World. For these reasons only a very brief discussion of the vegetation of the region and of the hotel garden will be given.

The preceding geological and climatic features interact with biotic factors to determine the vegetation of the C. Valles region. If we consider the area as a whole, three of the Mexican Vegetation Zones described by Leopold (1950) are present. The Thorn Forest vegetation zone is located east of the town on the coastal plain. In the foothills separating the town from the coastal plain is Tropical Deciduous Forest, and to the west of town is an area of Tropical Evergreen Forest. Ciudad Valles is located in a small valley covered primarily with plants of the Thorn Forest vegetation zone.

The garden of the Hotel Valles is extensive, surrounding nearly all of the buildings (Fig. 4). Areas of lawn with scattered trees are found in front of the buildings and in the central drive islands. The remainder of the garden is similar to a dense wood. There are few low

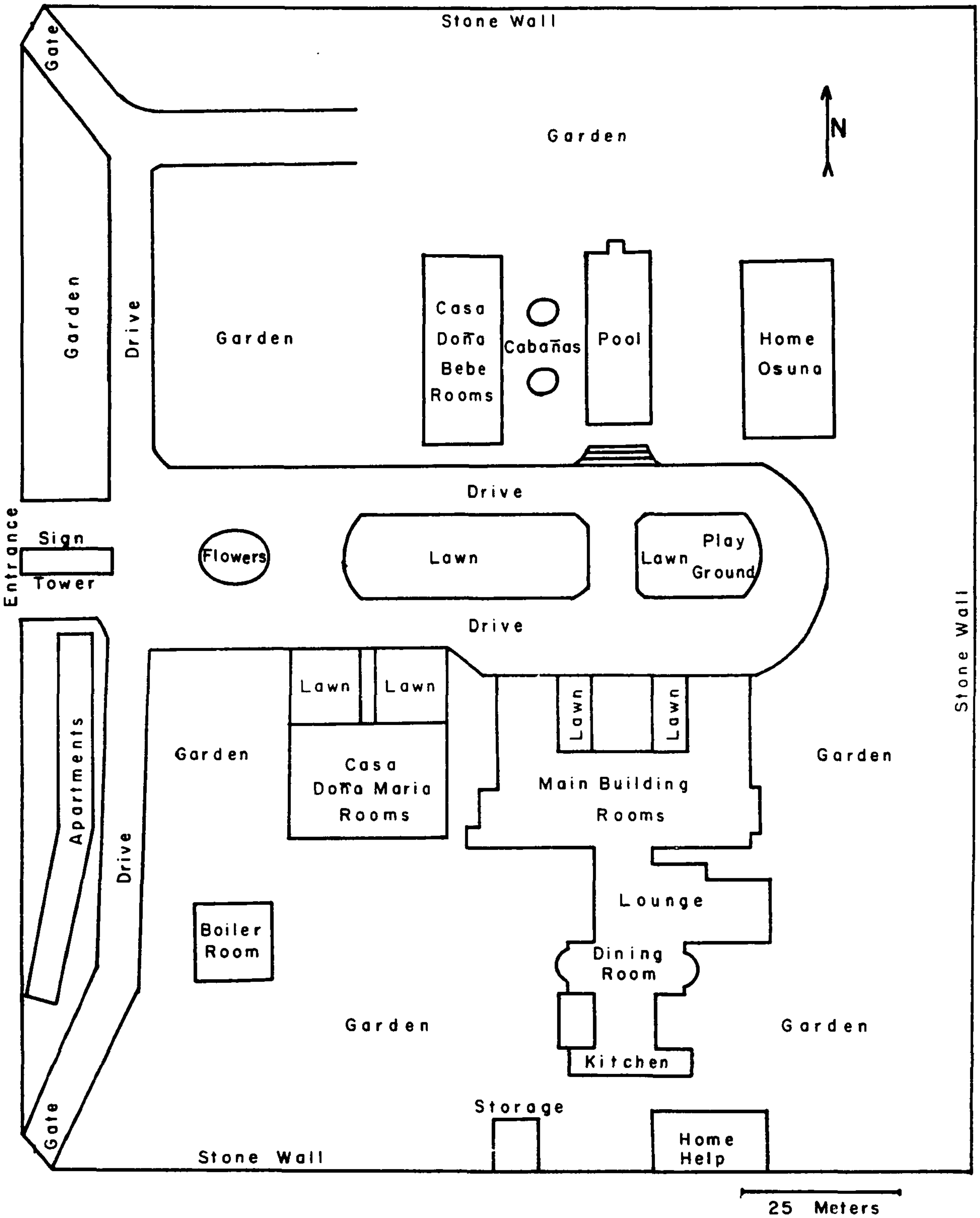


Fig. 4. Scale map of Hotel Valles and grounds, Ciudad Valles, S.L.P., Mexico, April 1969.

plants under the trees and little ground cover. This is due, in part, to the shady conditions and an intensive gardening campaign against leaves, litter, and weeds.

The plants in the garden were identified using Pesman's (1965) "Meet Flora Mexicana". The garden contains only a few native plants and many introduced varieties. The dominant tree, in terms of numbers, is flamboyan (*Delonix regia*) with tropical almond (*Terminalia catappa*) a close second. The tall decorative royal palm (*Sabal* sp.) is also numerous, and is found primarily in front of the hotel buildings and in the central drive area. Smaller trees; orange (*Citrus sinensis*), lemon (*C. limon*) and banana (*Platano musa*) are located in open areas of the garden. Climbing vines such as golden trumpet (*Allamanda cathartic*), bougainvillea (*Bougainvillea* sp.), and milkcup chalice vine (*Solandra nitida*) are planted near the buildings. Low plants, other than lawn, are few but some hibiscus (*Hibiscus rosachinensis*) are planted around the central drive.

Hotel and grounds

The study area was on the property of the Hotel Valles and was restricted by the boundaries of the hotel. Fig. 4 is a scale map of the hotel buildings and grounds. A two meter high stone wall outlines the 152 m by 183 m dimensions of the grounds. Ten separate stone buildings are situated within the confines of the property and are separated by areas of garden or lawn. The largest of these structures is the "Main Building" which is irregular in outline and whose greatest dimensions are 67 m in length by 48 m in width. The smallest building is a storage shed on the southern boundary of the land. This building is approximately six meters square. All buildings are constructed of stone with tile or thatch roofs.

Geckos were abundant on all the buildings but to increase efficiency study was concentrated on two buildings. The Main Building (Fig. 5 upper) was chosen because of good lighting, convenience, and a very large population of lizards. The general floor plan of this building can be seen in Fig. 4. The north end of the building consists of a U-shaped first floor porch and rooms. The central part of the building is composed of two floors of rooms, in the shape of a rectangle, and connected to the south end of this section is a kitchen-dining area. The building is constructed of rock with a roof of tile, except for the dining room, which is roofed with palm thatch. The second building chosen for concentrated study was the "Casa Doña María" (Fig. 4 and 5 lower). This building was chosen because of its location, good lighting, large population of lizards, and its construction, which contrasts nicely to the Main Building. The Doña María is a rectangular (25 m by 19 m), two story, structure directly to the west of the Main Building. Both levels have a continuous porch on their north, west and south sides. Construction is rock

Fig. 5. Main Building (upper) and Casa Doña María (lower), Hotel Valles study area, Ciudad Valles, S.L.P., Mexico, April 1969.

with a tile roof, but it differs from the Main Building in the extensive use of stucco under the porches.

Geckos were collected from nearly all structures on the grounds and comments will be made on other collecting localities in the section on habitat preference.

Methods and Materials

Period of study

The present study had its inception in May 1968 and continued through September 1969. During this period over 300 Hemidactylus frenatus were studied in the field and in the laboratory. These animals were members of a population located at the Hotel Valles in Ciudad Valles, Mexico.

A two day visit to C. Valles was made on 21 and 22 May 1968. This visit was exploratory and confirmed the feasibility of an ethoecological study of this population. Intensive field work was conducted during the three month period from 1 March to 30 May 1969. The last visit to the study area, in August 1969 (Aug. 23-26), was primarily for the collection of experimental animals.

Methods of working study area

On 1 March 1969 the field study was initiated in earnest. Portions of two buildings (Main Building and Doña María) were selected for a mark-recapture study and were carefully mapped, noting structural land marks, in order that lizard movements could be easily and accurately followed.

The method of study differed depending upon the types of data being collected. Ecological data were obtained by the usual capture, mark, and recapture method while behavioral data were gathered by observational means. Study usually began one hour before sunset and continued until two or three in the morning. On a number of nights this routine was altered by beginning work at two or three and continuing until an hour after sunrise. On five occasions work was continuous from one hour before sunset to one hour after sunrise.

Techniques of capture

The capture of geckos poses some unique problems to the investigator who is accustomed to working with diurnal lizards with limited climbing ability. Geckos are generally active in dim light conditions. The lizards are often difficult to see and once seen difficult to follow, especially if they move into darkened areas. These conditions necessitate the constant use of a flashlight or head lamp during capture procedures. The use of artificial light is a mixed blessing. Although it enables the collector to find and follow the lizards it also seems to stimulate the geckos to move, making capture more difficult. Another difficulty in live capture of geckos is their remarkable climbing ability. Lizards are commonly found high on walls and ceilings. Geckos low enough to be within reach moved quickly upward and beyond reach on the approach of the collector. A new method had to be developed to capture these animals.

Several methods were employed in the capture of lizards. Noosing was attempted early in the study. A slip noose of medium weight nylon fishing line was fastened at the tip of a fishing rod. This method was not very successful because the lizards carry their heads very near the substrate making it difficult to slip the noose over their heads, and the dim light conditions make it nearly impossible to see and handle the noose effectively.

Hand capture was also used and worked well on lizards that permitted approach. This was an especially useful method on juveniles and on adults, when within reach. Unfortunately most of the geckos were wary and could not be collected in this manner.

The most productive method of capture was one that was developed using a wisk broom at the end of a three meter bamboo pole. The gecko was sighted, swept off the wall or ceiling with the broom, and then captured by hand. This method was most successful when two persons worked together, but some lizards still managed to escape by seeking shelter in crevices, or because of darkness.

With repeated recaptures by any of the above methods the lizards became increasingly wary. Shy individuals would attempt to escape or seek shelter immediately upon sighting the collector. It was found that collecting success, and especially recapture success, was increased by use of intermittent periods of collection. The large number of people moving about the hotel acted to reduce wariness after only a few days of lessened collecting pressure.

Tail breakage during capture was common and will be discussed in the appropriate section. Other injuries as a result of capture were few and generally superficial. The most common of these were skin lacerations which resulted from abrasion caused by rubbing the lizard over the rough substrate. Lizards injured in this manner were often recaptured and found to be completely healed.

Procedures after capture

Measurements.--Immediately after capture measurements of cloacal temperatures were taken with a Schultheis quick-registering mercury bulb thermometer. The lizards were held with the ventral side up between the thumb and index finger. An attempt was made to grasp the lizards as near to the pectoral region as possible to insure that as little heat as possible was transferred from the collector's fingers to the body of the gecko. Temperatures of juveniles and sub-adults were not taken because of their small size. No temperatures were taken of lizards which had been chased a great distance because of the additional heat generated by vigorous activity and possible heat uptake or loss through contact with a markedly different environment

(Cowles and Bogert, 1944).

Substrate and air temperatures were taken at the place where the lizard had first been sighted. It has been pointed out (Mayhew, 1963) that accurate substrate temperatures are difficult to obtain because the bulb of the thermometer cannot be placed in contact with the substrate over its entire surface. In spite of this criticism it was thought that the inaccuracy of these temperatures would vary to the same degree and give an indication of the relation between substrate and body temperatures. Air temperatures were taken approximately two inches off the substrate at the place of first sighting. All temperatures were recorded to the nearest 0.1 C. Snout-vent and tail measurements to the nearest 0.1 mm were taken on the ventral surface of the animal using a Vernier calipers. Total weight measurements were made to the nearest 0.1 gm on a triple beam balance. All measurements were performed by one person on living animals.

Habitat data.--The date and time of capture were recorded as well as locality data. The exact location of the first sighting, and the height of this site, were noted. The orientation of substrate was recorded (e.g. vertical, horizontal) as well as the position of the lizard on the substrate (e.g. vertical head up, down, or horizontal.

Sex determination.--Sex determination is difficult in

Hemidactylus frenatus because of a lack of obvious dimorphic characters. The sex of adult animals was determined by a combination of characteristics. The larger size, the presence of more prominent femoral pores and the hemipenal swellings at the base of the tail served to distinguish the adult males. Juveniles were more difficult to sex but by using the presence of hemipenal swellings males could generally be recognized. Sex was determined with a reasonably high degree of accuracy and on only five occasions was it necessary to change the determination made on first capture.

Marking

A modification of the toe-clipping method of Martof (1953) and a system using colored paints were used to identify animals. Each lizard was individually and permanently marked for future recognition by removing toes with scissors. The system required the removal of from one to six toes, but the maximum number removed from any one foot was two. This method of toe clipping is summarized in Table 2. When a single toe was cut, such as in animals numbered 1, 10 or 100, a special code was utilized as a "zero" mark on the opposite leg. This mark utilized the second and fourth digits, a combination not used to indicate a number. The use of the "zero" mark prevented confusion that might arise with the capture of a lizard having a toe missing through natural causes. The system permitted the marking

Table 2. Code for marking lizards by toe-clipping. Symbol (1) represents an entire digit; the (0) represents a clipped toe.

	Fore Limbs		Hind Limbs	
Number	Left	Right	Left	Right
1	11110	10101*	11111	11111
3	11011	10101*	11111	11111
6	01110	11111	11111	11111
9	00111	11111	11111	11111
10	10101*	01111	11111	11111
60	11111	01110	11111	11111
66	01110	01110	11111	11111
100	11111	11111	11110	10101*
160	11111	01110	11110	11111
166	01110	01110	11110	11111

* Zero mark, explained in text.

of 999 lizards which was more than adequate for this study. The toe clip did not appear to affect the climbing ability or survival of the marked animals, and it provided a relatively error free system of marking.

To assist in identification of animals from a distance some adults were conspicuously marked by painting colored dots, in various combinations, on their backs and legs. Two colors of radiant fluorescent paint were used (Radiant Color Co., Richmond, Calif.). Under natural light this paint looks very much like any other paint but under black light it fluoresces. The use of this paint and a black light (Black Light Specialities, Okla. City) enabled the investigator to see and recognize individual geckos under dim light conditions.

Male and female H. frenatus were color coded with orange and yellow respectively. Numbers from one to nine were indicated by corresponding numbers of daubs of paint on the lizard's backs, number 10 by painting the upper surface of the left foreleg, and number 11 with painted foreleg plus one daub on the back. Number 20 was indicated by painting the upper right foreleg, number 30 the upper left hindleg and number 40 the upper right hindleg. Juveniles and subadults were marked with a stripe down the midback, and naimals from the Doña María were distinguished from Main building animals by a band across the base of the tail. By means of this system a total of 49 adult lizards could be individually marked, on each building.

Two factors limited the effectiveness of the paint marking system. The small granular scales of *H. frenatus* did not allow the paint to penetrate and hold as well as it might on a large scaled species, and after about three weeks the marks began to flake off and had to be replaced. The shedding of the skin with the concomitant loss of paint markings also had to be reckoned with.

The effect of the paint marks upon survival cannot be evaluated because it is not known if the marks exposed the lizards to greater predation pressures. It is known that, in the absence of strong artificial light, lizards with paint marks were no more evident to the human eye than those without marks.

Collection of behavioral data

Two well lighted areas with large populations of geckos were chosen on the Main Building and the Doña María respectively for behavioral observation. An attempt was made to individually paint mark these animals to aid in interpretation of observed behavior. This was found to be difficult because animals which occupied unobstructed areas suitable for observation were wary. In spite of this difficulty some animals were marked and subsequently came under observation. The investigator placed himself about six meters from the area under observation about half an hour before sunset. If no quick movements were made the emerging geckos did not appear to notice the presence of the investigator and observation could be accomplished with the aid of seven power binoculars. Behavioral observations were generally made on alternate nights. The period of time the lizards were watched varied from only a few hours to nearly 10 hours.

Results and Discussion

Sex ratio

The sex ratio for 130 male and 156 female *H. frenatus* was 45:55. The ratio is approximately the same for animals under 45 mm (43:57) and those over 45 mm (46:54)(Table 3). A Chi-square test of significance was used to compare these data with the expected 50:50 sex ratio. No significant difference from the expected is seen in either of the size classes, or for the total number of animals collected.

The secondary sex ratio (ratio at birth) can not be ascertained without actual birth records, but of 14 animals under 35 mm in snout-vent length, equal numbers of males and females were found. The small number of records and the difficulty of sexing these tiny animals sheds some doubt on this data.

In most studies on breeding structure of lizard populations it has been found that females outnumber males. This has been shown in iguanids by Blair (1960), Hirth (1963), and Tinkle (1967); and in agamids by Harris (1964).

Table 3. Sex ratios of Hemidactylus frenatus by size class with results of Chi-square tests.* Ciudad Valles, S.L.P., Mexico, March-May 1969.

	Snout-vent Length		
	Less Than 45 mm	More Than 45 mm	All Animals
Total No. of Animals	42	244	286
No. of Males	18	112	130
Percent Males	43	46	45
P Value	.500>P>.250	.250>P>.100	.250>P>.100

* Chi-square values were used to test the hypothesis of a 50:50 sex ratio.

The percentage of females in these studies varies from only slightly over 50% in Uta stansburiana to 63% in Sceloporus olivaceus. Work with gekkonid lizards also indicates an uneven sex ratio in favor of females (Church, 1962; Greer, 1967; Rose and Barbour, 1968). The sex ratio in these studies varies to approximately the same degree as in iguanids and agamids. In the few lizard studies in which secondary sex ratio is reported a ratio near 50:50 is generally found (Blair, 1960; Tinkle, 1967). No reports of secondary sex ratios in gekkonid lizards have been published.

Church (1962), in his study of H. frenatus found that 375 of 923 animals were males (41%). In view of these data and the results of the present study it is felt that a significantly greater number of adult females exist in breeding populations of H. frenatus.

If we assume that the secondary sex ratio is equal in H. frenatus then something is causing differential survival in these populations. The direct causes are unknown, but it is possible that the males are more active and therefore exposed to more attacks of predators. Antagonism between males could make establishment of a territory difficult for a maturing male, resulting in continued wandering in search of a place to settle. Wandering in unfamiliar areas could result in greater susceptibility to predators than would be found in individuals with established territories.

A possible biological advantage of this unequal sex ratio in H. frenatus is apparent if we assume harems or promiscuous mating. If one male could service a number of females the survival of an equal number of males and females would be a waste of food, home sites and other requirements. It would be a selective advantage to the population to have surplus males taken by predators, thereby reducing predator pressure on valuable females.

Size

The body length of the sexes differed, with males being larger than females. The mean snout-vent length for 130 males was 51.0 mm while the female average for 130 individuals was 50.0 mm. These means were significantly different at the $P < .001$ level. The 95% confidence limits for the mean of males and females were 49.65 - 52.35 mm, and 49.12 - 50.88 mm respectively.

The weight of the sexes also differed with the males again being larger. It should be pointed out that some animals had missing or partially regenerated tails at weighing. Inaccuracies as a result of this factor are thought to be minimal, since the sexes have been shown to have an equal chance of possessing shed or regenerated tails. The average weight of 128 males was 3.2 gm and the average for females 2.9 gm. The means were significantly different at the $P < .001$ level. The 95% confidence limits for the mean of males and females were 3.0 - 3.4 gm and

2.78 - 3.02 gm respectively.

Weights and lengths of hatchlings were not obtained but some idea of size at hatching can be gained by looking at the records of the smallest animals collected. The smallest male was 21.4 mm in snout-vent length and weighed 0.3 gm. The smallest female was a 24.0 mm, 0.3 gm individual. The lightest animal collected, a male, weighed 0.15 gm and was 22.2 mm in length. The snout-vent length at hatching is probably very close to 21.4 mm because this animal still had an open umbilical scar. The weight at hatching is, no doubt, closer to 0.3 gm than the lighter (.15 gm) weight recorded for a longer animal. It is likely that the hatchlings will tend to lose weight after emerging from the eggs due to energy expenditure and difficulty in obtaining food. Size differences between the sexes at hatching can not be demonstrated with the small number of records, but studies on non-gekkonids report no differences between the sexes (Blair, 1960; Tinkle, 1967).

Church (1962) published length and weight data for _H. frenatus_ in Bandung, Java. He reported mean snout-vent lengths for 375 males and 548 females of 54.48 mm and 51.37 mm respectively. Average weights of 3.10 gm for males and 2.54 gm for females were also given. Church's weight and length data are higher than those reported in the present study. The length of the Java animals ranged from 35 - 67 mm while the range in the present study was from 21.4 to

61 mm. The weight ranges also differed to a similar degree (0.6 - 5.6 gm Java and .15 - 5.5 gm Mexico). It is apparent that the H. frenatus in Java are larger than those from C. Valles, Mexico.

The reasons for this size difference are not known, but it is possible that they are related to the geographic position of the two populations. The C. Valles population is located 23° N latitude while the Java population is at 8° S latitude. This proximity of Java to the equator probably assures that the weather is more conducive to gecko growth than it is in northern Mexico. The absolute variation in temperature over a year in Bandung, Java was only 18.2 C (Church, 1962), while the variation over the three month study period in C. Valles was 22.2 C (Table 1). The Mexican population has to withstand daily and seasonal weather fluctuations which slow development, decrease feeding time, and probably also reduce the life span of the geckos.

Fig. 6 shows weight frequencies of H. frenatus. The disproportionately large number of females as well as the greater weight of the males can be seen in this figure. Age classes are difficult to ascertain from the frequency distribution. Several factors are operating to obscure age classes. First, there is evidence that individuals in the population are long-lived and reach adult size in one year. Second, the reproductive season extends from early

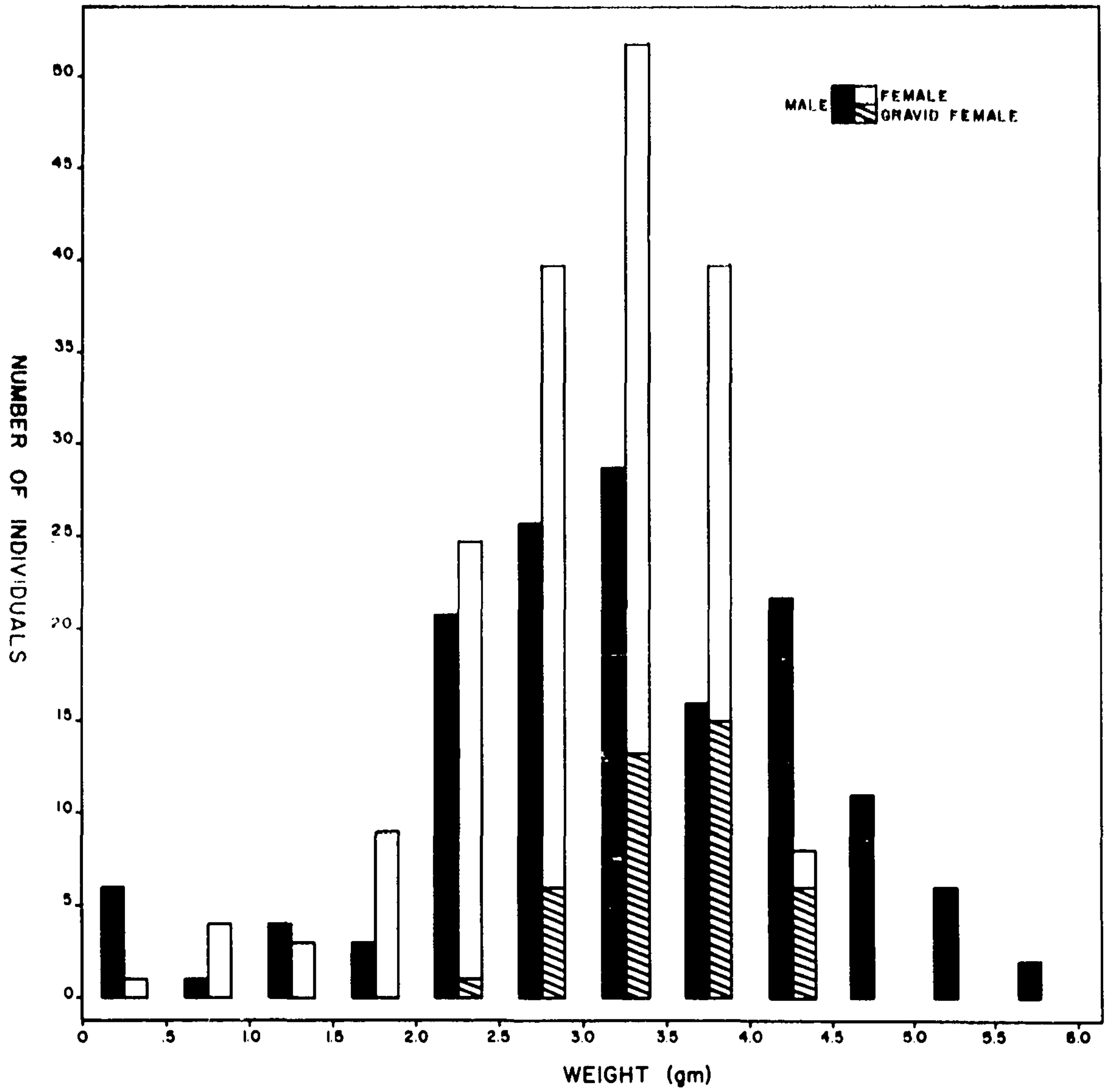


Fig. 6. Weight frequencies of 327 *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico, March-May 1969.

February to October or November (Thomas Osuna, personal communication). Young produced over such a long span of time result in a wide distribution of weight frequencies.

The frequency of gravid females in various weight classes is also shown in Fig. 6. The majority of females (167 of 182) fall in these sexually mature weight classes. The snout-vent lengths of gravid females ranged from 47.3 - 56.0 mm and Fig. 6 demonstrates that this range also includes the majority of females captured. The proportionately large number of reproductively active females in the population could be an advantage in a species such as *H. frenatus* in which only one or two eggs per clutch are produced.

The weight - snout-vent length relationships for 350 geckos are plotted in Fig. 7. If an imaginary line is drawn through the distribution a nearly uniform curve is obtained. The only deviations being in the smaller animals in which length increases more rapidly than weight, and in an obvious decrease in growth as the lizards approach mature size. Very little difference exists between the weights of males and females of the same length. The wide variation of weight at a given snout-vent length is striking. In females this could be explained by the presence of gravid individuals, but the females do not seem to vary more than males. The weight variation is probably due to differential amounts of stored food in the form of fat,

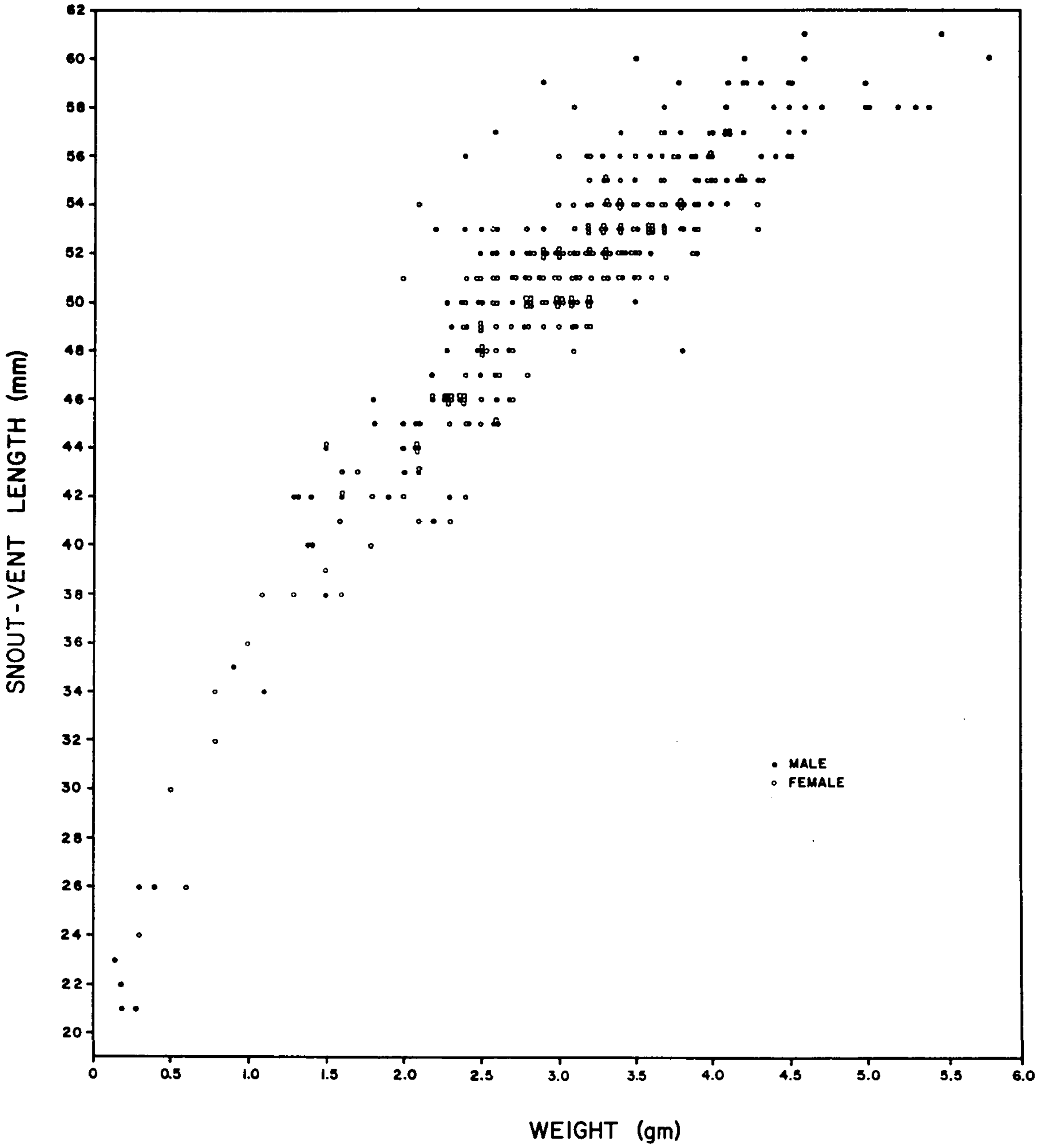


Fig. 7. Correlation of weight with snout-vent length of 350 Hemidactylus frenatus collected at Ciudad Valles, S.L.P., Mexico, March-May 1969.

and to differences in the condition of the tail (missing, partially regenerated, etc.).

Growth

Growth rates per month by snout-vent length and sex are presented in Table 4. A t-test for the difference between means was used to test possible sexual differences in growth rate in all three size classes. No significant difference was found in the two smallest size classes, but in the 51-60 mm size class a significant difference between the means of the sexes at the $P < .01$ level was obtained. This difference in the largest size class can be explained by a slowing of female growth as they approach adult size. Males are larger as adults and therefore maintain a greater growth rate in this size class.

Tinkle (1967) in a literature review of lizard growth, states that "there are no very significant differences reported in the literature between growth rates of males and females". This statement agrees with the results given above.

The combined average monthly growth rates give a better indication of growth in the three size classes because of larger sample size. The average growth of animals in the 30-40 mm size class was 4.4 ± 2.05 mm. The growth per month in the 41-50 and 51-60 mm size classes was 2.1 ± .35, .97 ± .255 mm respectively. The combined average growth rates were significantly different at the

Table 4. Average growth rate per month by sex and snout-vent length for *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico, March-May 1969.

	Males		Females		Both Sexes
Size Group(mm)	Number of Lizards in Sample	Average Growth Per Month(mm)	Number of Lizards in Sample	Average Growth Per Month(mm)	Average Growth Per Month(mm)
31-40	2	6.3	2	2.5	4.4
41-50	8	1.9	13	2.3	2.1
51-60	8	1.6	16	0.35	0.97

$P < .001$ level. These rates fit the classic idea of animal growth with very rapid growth at first and a gradual slowing as maturity is reached.

Tinkle's (1967) review of lizard growth shows that growth rates average approximately 0.2 - 0.3 mm per day. Cagle (1946a) indicated growth rates for *Hemidactylus garnoti* of .61 mm per day maximum and at least .20 mm per day until mature. Bustard (1968a) reported growth rates of .05 mm per day in adult and subadult *Gehyra variegata*. If the monthly growth rates in Table 4 are converted to daily values only one of them (males 30-40 mm, .21 mm per day) is as high as the figures of Tinkle and Cagle, but most of them are higher than Bustard's values.

The growth rate differences above may be actual species differences or they may be related to temperature differences in the habitats of the species studied. Bustard (1968a) states that growth rate increases directly with temperature in ectothermic animals. These factors plus the lack of growth records for hatchling and juvenile *H. frenatus* could explain the discrepancies in growth rates.

Tail

The tail is an organ of great importance in lizards, functioning in fat storage, predator escape, balance, and mating.

Length.--In *H. frenatus* that have never sustained a broken tail the ratio of snout-vent length to tail length varies from about 1.2 to .99 mm in males, and from .98 to 1.1 mm in females. If the mean tail length for each snout-vent class is graphed ontogenetic changes can be observed (Fig. 8). In males the tail appears to be proportionately shorter in adults than in young, but in females the opposite condition holds, tails are proportionately longer in adults and shorter in young. The significance of this sexual difference is not known.

The longest unbroken tail recorded for a female was one of 56.9 mm possessed by a lizard with a snout-vent length of 54 mm. The snout-vent : tail length ratio was .95. The longest male tail was one of 63.2 mm on a lizard with a snout-vent length of 64.5 mm. This body was 1.02 times the tail length of the lizard.

Reports of lizard snout-vent : tail length ratios are scarce, but if a generalization can be made, it is that tails are longer than bodies. This is especially true in arboreal lizards such as _Anolis nebulosus_ (Jenssen, 1969) and _Sceloporus olivaceus_ (Blair, 1960), but it is also true of completely terrestrial lizards such as _Uta stansburiana_ (Tinkle, 1967) and _Eumeces fasciatus_ (Fitch, 1954). Rose and Barbour (1968), working with _Hemidactylus turcicus_, reported tail length : snout-vent length ratios of .94 for juveniles, .96 for subadults, and 1.07 for adults. Few other snout-vent : tail length ratios have been reported for geckos but it appears from the present work, and the

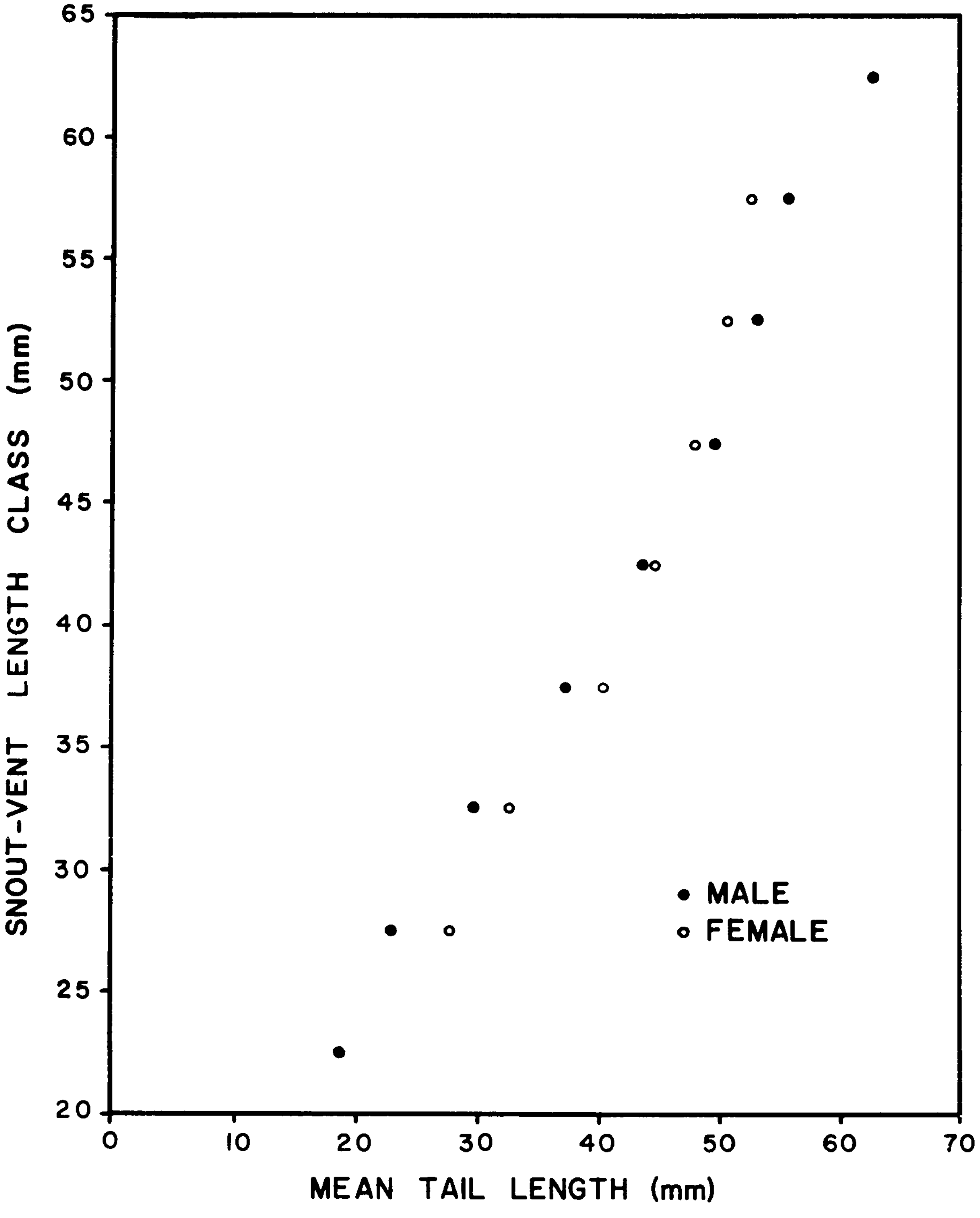


Fig. 8. Tail length plotted against snout-vent length for 147 Hemidactylus frenatus from Ciudad Valles, S.L.P., Mexico, March-May 1969.

work of Rose and Barbour, that the generalization of tails longer than bodies may not hold for the family Gekkonidae.

Breakage.--In spite of its usefulness the tail is a potential liability when the lizard is attacked by a predator. Geckos share, with many other lizards, a fragile tail construction which permits easy breakage when grasped by a predator or aggressor.

The anatomical basis of tail breakage has been described by Warner (1961). In *Hemidactylus* the tail begins with 5 non-autotomous pygal vertebrae which are followed by autotomous (except for the last three) postpygals. Each vertebra is divided in the midvertebral plane by a preformed autotomy split. The non-skeletal caudal structures are similarly divided, and the autotomy plane is found in all caudal organs and tissues except perhaps the spinal cord. It is generally accepted that the tail breaks at one of these intersegmental planes of weakness rather than between vertebrae (Bellairs, 1957).

The frequency of broken or regenerated tails in the population should be proportional to frequency of attacks by predators, but the picture is complicated by the fact that tails can be broken in other ways. Fighting or mating animals often grab tails, resulting in breakage. Collectors also often break tails in the process of capture.

Field observations were made on some possible causes of natural tail breakage in *H. frenatus*. On 5 April 1969 at 7:34 PM a group of marked geckos on the upper west porch of the Doña María were under observation. A large male approached another smaller male who responded by running off. The larger male pursued and grabbed the smaller animal by the center of the tail. The smaller began to quiver in the grasp of the larger lizard, gave a strong jerk, and escaped. On 10 April 1969 at 7:30 PM another group of Doña María geckos were under observation. A large male was approached by an adult female, and as she came within 10 cm the male lunged and grabbed for her. She turned to flee and the male grasped her tail near the end. The female was stopped short and began to quiver as she struggled to escape. The male appeared to try to shift his grip and the female jerked free and escaped. Although no tail breakage occurred, these two observations are probably representative of some of the causes of natural tail breakage in H. frenatus.

Evidence of natural tail breakage was found in all ages of lizards. The frequencies of tail breakage by sex and type of breakage are shown in Table 5. Thirty nine per cent of the males and 36% of the females suffered natural tail breakage. A Chi-square test of independence was performed to determine if sexual differences exist in frequency of breakage. Sexual differences in total breakage, breakage in capture, and natural breakage were found to be nonsignificant. Frequency of natural breakage for

Table 5. Frequency of tail breakage by sex and type of breakage in *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico, March-May 1969.

	Males	Females	Both Sexes
No. Broken in Nature	57	60	117
No. Broken in Capture	18	32	50
Total Broken	75	92	167
Unbroken	73	74	147
Total No. Captures	148	166	314
Per Cent Broken in Nature	39	36	37
Per Cent Broken in Capture	12	19	16
Per Cent Broken Overall	51	55	53

the population as a whole was 37.5%. Thus the value of autotomy as an escape mechanism appears relatively high.

Natural tail breakage frequency was determined for animals more than, and less than, 50 mm in snout-vent length. Thirty-six per cent (37 of 101) of the less than 50 mm animals had broken or regenerated tails while 53% (87 of 163) of the more than 50 mm animals had suffered tail breakage.

The literature on frequency of tail breakage in geckos is fairly extensive. The rare gecko of the genus *Agamura* apparently does not lose its tail at all (Blanford, 1876), but in other geckos the frequency of regeneration varies from 60% in *Gehyra variegata* (Bustard, 1968a) to nine per cent in *Diplodactylus williamsi* (Bustard, 1964). In the genus *Hemidactylus*, tail breakage frequency varies from 61.2% in *H. turcicus* (Werner, 1968) to 31% in *H. garnotii* (Cagle, 1946b). Some of the above data, such as that of Werner were obtained from preserved specimens whose tail loss may have occurred during or after collection, resulting in higher frequencies than are naturally present. Higher frequencies can be obtained in the present study if breakage during capture is included. Fifty-three per cent of the *H. frenatus* had broken or regenerated tails if we include the breaks that occurred in capture.

Sexual and ontogenetic differences in frequency of tail breakage have been investigated by Cagle (1946b) and

Werner (1968). Cagle reported that only 10% of juvenile H. garnotii had regenerated or broken tails while 31% of the adults possessed regenerated or broken tails. Werner also found that juvenile H. turcicus had a lower frequency of tail breakage than adults (juveniles 54% and adults 65%). Cagle and Werner both found no significant differences between the sexes in frequency of tail breakage, although in both studies males had a slightly higher frequency than females. The published data for tail breakage frequency of gekkonids seems to agree very well with the data from the present study.

Shedding

No data were obtained on shedding frequency, but many captive animals went through ecdysis and a few observations were made. The approach of the molt is signalled by the opaque, lifeless appearance of the skin. The old, cornified epidermis loosens and begins to split along the sides of the body and head. Suture lines also form around the bases of the legs and tail. The dorsal and ventral halves of the body and head skin are removed with the aid of the mouth and by rubbing on nearby objects. The skin of the legs and tail is pulled or rolled off with the mouth, much like gloves. All skin is generally eaten after removal. The approximate duration of the molt was determined for three captive animals and found to be one day or less.

Only one free-living gecko was captured while in the process of shedding, and this animal was in the early stages of molt. This seemed unusual since the generalization has been made (Tinkle, 1967) that lizards molt every three or four weeks. If this were the case the probability of capturing a molting individual would be much greater than one in over 500 captures and recaptures. Observations on captive shedding animals provided an explanation for this scarcity of shedding individuals in a natural population. It was found that the geckos' ability to climb is adversely affected by the molt. Animals in the latter stages of molt cannot cling to vertical surfaces or ceilings, but are still able to walk upright on a horizontal surface. Geckos unable to climb would be exposed to much greater predation pressures than those able to climb, and it would be a selective advantage to remain quiescent during this period. The situation has parallels in snakes and many water birds. The eyesight of snakes is adversely affected during ecdysis and they are generally quiescent until shedding is completed. Molting water birds are unable to fly because they lose all their wing primaries at once. Birds in this condition are often quite secretive until molt is completed.

Population density and biomass

H. frenatus was abundant on the buildings and grounds of the Hotel Valles. The lizards were found on every building and were even on light poles and trees in the gardens. Although collecting was restricted to limited sections of two buildings a total of 310 geckos were marked during the study period.

Population density is defined by Odum (1959) as population size in relation to some unit of space. Population size was estimated using a mark-recapture method in which a sample of the population was captured, marked and released, and a proportion used to estimate the total population (Table 6). The pre-census and census dates were chosen because they occurred during a period of high lizard activity, and because nearly equal numbers of lizards were caught on pre-census and census dates. The porportion was set up following the procedure developed by Peterson (1896) and estimates of population size for limited areas of two buildings were determined (Table 7).

The ideas involved in the proportional method of population size estimation are simple enough but certain assumptions are implied when this method is used. These are discussed in detail by Andrewartha (1961) and were given careful consideration by the author.

The approximate floor area of the census area was 1758 sq ft in the Main Building and 4656 sq ft in the Doña María. Using the population size estimates this extrapolates to 6200 individuals per acre on the Main Building and 1026 individuals per acre on the Doña María. The mean

Table 6. Estimated number of Hemidactylus frenatus present in two census areas at the Hotel Valles, Ciudad Valles, S.L.P., Mexico during March 1969.

Precensus Dates 1969 (A)	Census Dates (B)	No. Marked on (A)	Total No. Captured on (B)	Recaptures on (B)	Population Estimate for (A)
Main Building					
3/4-3/22	3/30-4/14	69	54	15	248
Doña María					
3/8-3/22	3/29-4/7	37	37	12	114

Table 7. Estimated density and biomass of Hemidactylus frenatus on two census areas at the Hotel Valles, Ciudad Valles, S.L.P., Mexico during March 1969.

	Main Building	Doña María
Estimated Number of Lizards (from Table 6)	248	114
Approximate Area of Habitat (sq ft)	1758	4656
Density (individuals/acre)	6200	1026
Biomass (gm/acre)	18,600	3078

weight for males was 3.2 gm and for females 2.9 gm with an average weight of 3.0 gm. Biomass in grams per acre was estimated from these values and found to be 18,600 gm per acre on the Main Building and 3078 gm per acre on the Doña María (Table 7).

The population size estimate on the Doña María census area (114) was much closer to the number actually captured (98) than was the size estimate on the Main Building census area (248 estimated to 179 captured), and the density and biomass estimates on the Doña María were much lower values than those for the Main Building. It is thought that these differences are a result of contrasts in the habitats provided by the two census areas.

The Doña María census area is a fairly modern, well lighted, stucco and rock porch. The roof of the porch is uncomplicated by rafters and has few cracks, crevices or holes. The census area of the Main Building is an old, poorly lighted, rock and wood porch. The roof is constructed of wood with rafters spaced at five foot intervals, and has numerous cracks, crevices and holes. The complex environment of the Main Building, in spite of its smaller size, supports many more lizards than does the Doña María area, and the lizards are much more difficult to capture than those on the Doña María. This results in a larger proportion of the Doña María population being captured, and in smaller density and biomass estimates for this census area.

Published density estimates in lizards other than gekkonids have ranged from two per acre in Basiliscus vittatus (Hirth, 1963) to 600 per acre in Anolis limifrons (Heatwole and Sexton, 1966). Biomass estimates of non-gekkonid lizards have been few in number. Tinkle (1967) reported a maximum biomass of 143 grams per acre in Uta and Jenssen (1969) estimates a maximum of 488 gm per acre in Anolis nebulosus. In gekkonids, Cagle (1946a) has reported a density of 500 Hemidactylus garnoti in a 2400 sq ft area.

Although species comparisons are complicated by differences in body size, it appears that geckos and Anolis have higher density and biomass values than other lizards. These relatively high values can be explained by the presence of multiple dimensions in the habitats of these lizards. Many geckos and Anolis can utilize vertical as well as horizontal surfaces which greatly increases the carrying capacity of a given two dimensional area.

Thermal relationships

The early study by Cowles and Bogert (1944), dealing with temperature relations in desert reptiles, has stimulated a great deal of work on body temperatures of reptiles. The reviews of this work by Bogert (1949), Fitch (1956), Schmidt-Nielsen and Dawson (1964), Brattstrom (1965) and Fry (1967) demonstrate that little consideration has been given to the ecological significance of temperature measurements. Some authors have, however, attempted to relate their work on temperature preference to the ecology of the lizard concerned (e.g., Bogert, 1949; Inger, 1959; Rand, 1964; Ruibal, 1961).

In the past, most of the species studied have been temperate forms, and the bulk of the work has been on species from semiarid regions. The statement of St. Girons and St. Girons (1956), that little is known about the thermal requirements of tropical reptiles, is still largely true. If we consider tropical nocturnal reptiles, such as H. frenatus, virtually nothing is known about their thermal ecology.

In the present study cloacal temperatures were taken of 221 H. frenatus. Male cloacal temperatures averaged 27.1 ± 3.46 C (95% confidence limits; 26.20 and 27.80 C) while females averaged 27.3 ± 3.0 C (95% confidence limits; 26.80 and 27.80 C). The mean cloacal temperature for females was slightly higher than for males but the difference was not significant. The average cloacal temperature for both sexes was 27.2 ± 3.19 C with a range from 19.0 to 34.3 C.

The voluntary minimum and voluntary maximum temperatures were probably not determined. The lowest cloacal temperature (19.0 C) was obtained from a 42 mm, Main Building female on 4 March. The air temperature and substrate temperatures at the site of capture were 16.2 and 18.0 C respectively. The animal was on a wooden substrate 3.5 m high near the juncture of the ceiling and wall. The highest cloacal temperature recorded was 34.3 C from a 56.0 mm male captured on the upper west porch of the Doña María on 16 April. The air temperature at the site of capture was 31.6 C and the substrate temperature 32.4 C. The animal was resting near the ceiling on the stucco wall 4.9 m above floor level. Geckos were active at the temperature extremes encountered during the three month study period, and it is felt that work done throughout the year would greatly extend both the voluntary minimum and voluntary maximum temperatures for this species.

Air, substrate, and cloacal temperatures were taken concurrently for 138 captures of active geckos. Average cloacal temperature was higher than the average air or substrate temperatures, and the means were compared using t-tests (Table 8). Significant differences at the $P < .001$ level were obtained between the cloacal temperatures and the two environmental temperatures.

The degree of correlation between cloacal temperature and the two environmental temperatures can be seen in Figs. 9 and 10. In both cases the correlation coefficient is very high, and the probability of correlation highly significant.

In nearly every case the cloacal temperature is higher

Table 8. Air, cloacal, and substrate temperature data with t-values for the differences between the means for 138 captures of *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico, March-May 1969.

	Mean	Range	Standard Deviation	t Value
Air	26.9	16.0-33.4	3.65	3.43*
Cloacal	28.4	19.0-34.3	3.61	3.69*
Substrate	26.8	18.0-34.3	3.57	

* Significantly different at the .001 level.

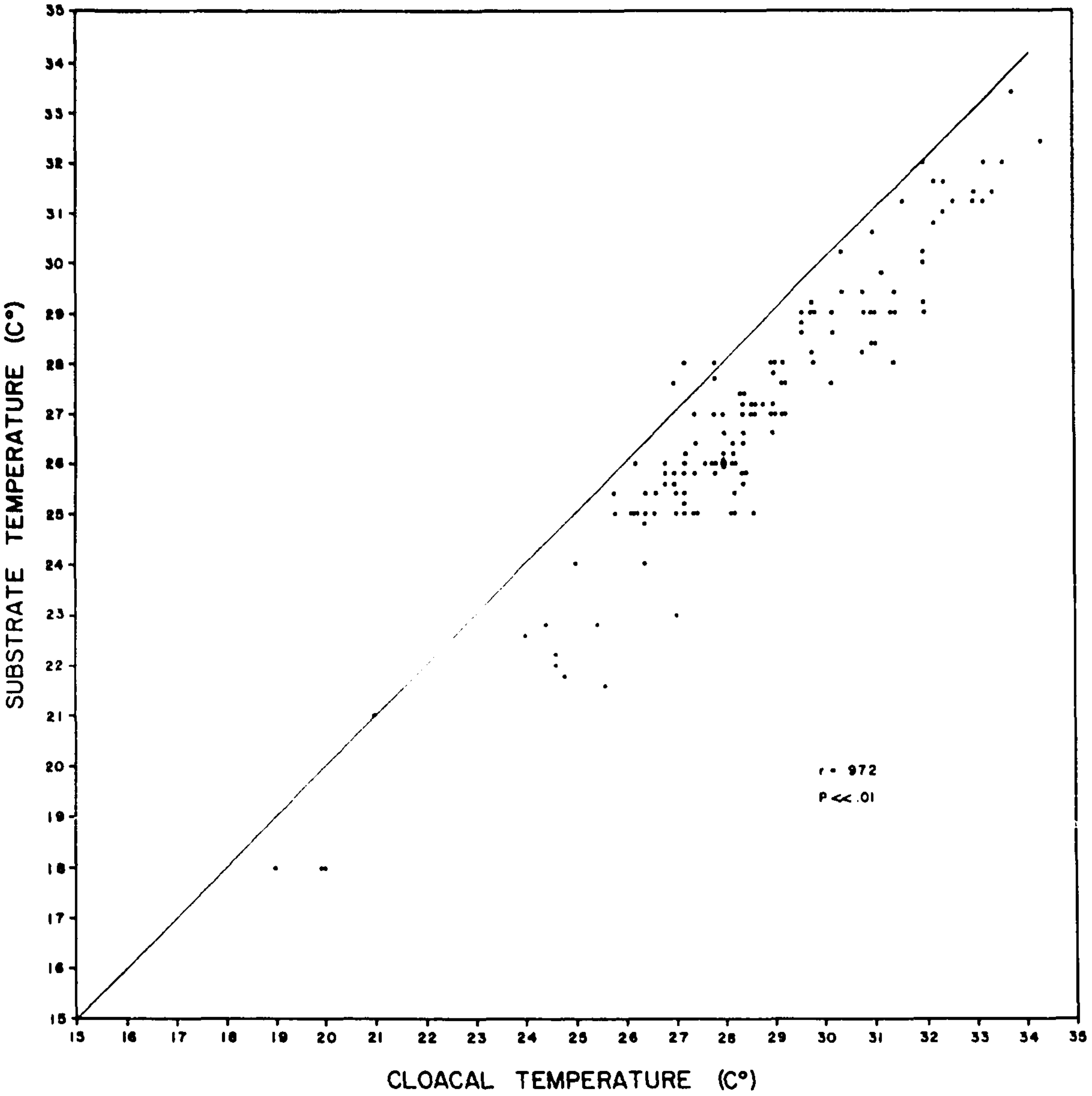


Fig. 9. Scatter diagram of cloacal temperatures and substrate temperatures of Hemidactylus frenatus from Ciudad Valles, S.L.P., Mexico, March-May 1969. The line connects the isothermal points. r = the product moment correlation coefficient; P = the probability of the correlation.

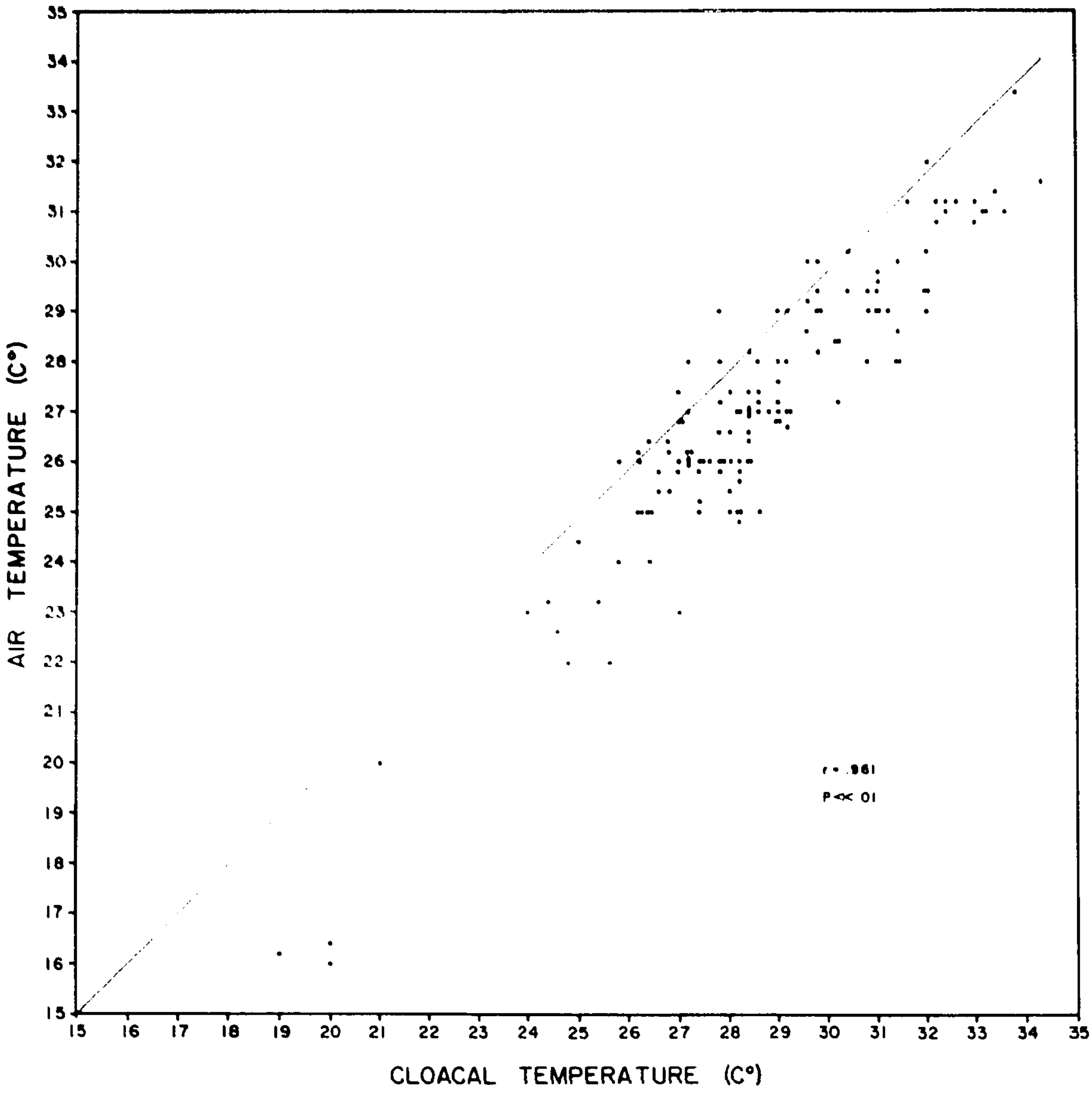


Fig. 10. Scatter diagram of cloacal temperatures and air temperatures of *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico, March-May 1969. The line connects the isothermal points. r = the product moment correlation coefficient; P = the probability of the correlation.

than either the substrate or the air temperature. The maximum positive deviation of cloacal temperature above air and substrate was approximately four degrees centigrade. The maximum negative deviations of cloacal temperatures below air and substrate temperatures were only 1.2 and 0.8 C respectively.

Two reasons for higher cloacal temperatures can be proposed. First, it is possible that metabolic heat is responsible, but it has been demonstrated that lizards gain little heat in this manner (Templeton, 1960). Second, and probably a more reasonable explanation is that geckos use behavioral means to maintain a slightly higher body temperature. The animals may seek warmer areas of substrate and pockets of warm air, or individuals can change the orientation of their body to the substrate in order to maintain a slightly higher body temperature.

A visual comparison of the scatter diagrams and correlation coefficients seems to show a higher degree of correlation between cloacal temperature and substrate temperature than between cloacal temperature and air temperature. A test of homogeneity for the two correlation coefficients was non-significant (Sokal and Rohlf, 1969) and statistically we must reject the hypothesis that the r-values differ. Geckos are highly thigmotatic and are generally closely associated with the substrate, having at least the ventral surface of their bodies tightly pressed to it.

Animals often wedge themselves in the juncture of wall and ceiling, thereby applying more body surface to the substrate. For these reasons conduction from the substrate probably plays a greater part in determining cloacal temperature than convection from the air (especially when nights are still). The higher correlation coefficient between substrate and cloacal temperatures is probably a real difference, and if greater sample sizes were used it would be significantly different from the cloacal-air correlation coefficient.

Table 9 compares temperature data of seven diverse groups of diurnal lizards with H. frenatus. The gecko has a much lower mean temperature than the others, and the lower limits of the ranges of six of the groups does not even include the mean of H. frenatus. H. frenatus also has a much larger range and greater standard deviation than all but the Anolis. The differences in variability are even more striking if it is realized that data for a single species are being compared with data from groups composed of more than one species and even more than one genus. These differences are obviously directly related to the fact that nocturnal lizards have only limited thermoregulatory abilities and possibilities. Diurnal lizards can utilize radiant energy by basking to circumvent daily, monthly and seasonal temperature variations. The lack of a consistent and readily available external heat source

Table 9. Comparison of temperature data of seven groups of diurnal lizards with data from *Hemidactylus frenatus*.*

Group	Species Investigated No. Species in Group	Mean (Range)	Standard Deviation
Crotaphytus	2/5	38.1 (37.5-38.7)	.72
Callisaurus-*Uma*-*Holbrookia*	3/7	38.5 (38.4-38.6)	.10
Uta	2/10	35.9 (35.6-36.2)	.18
Phrynosoma	3/14	36.2 (34.9-36.9)	1.27
Cnemidophorus	4/18	40.7 (39.9-41.3)	.37
Sceloporus	12/100	34.9 (32.9-36.9)	1.25
Anolis	5/250	31.3 (24.8-36.6)	3.54
Hemidactylus frenatus	1/76	28.4 (19.0-34.3)	3.19

* Data from Soule, 1963, except for *Anolis* and *H. frenatus*. *Anolis* data from Rubal, 1961 and *H. frenatus* data from this paper.

makes _H. frenatus_ directly dependent upon variable ambient temperatures.

Literature dealing with temperature relations in nocturnal gekkonid lizards is very limited and much of the work has been done in thermal gradients (Licht et al, 1966a), and on heat resistance (Licht et al, 1966b). The sparse data dealing with animals in the field are restricted to a few reports of cloacal temperatures of geckos in their diurnal retreats (Bustar, 1967a; Brattstrom, 1965; Licht et al, 1966a), and some cloacal temperatures taken from active nocturnal geckos (Brattstrom, 1965). The work above has largely been done on gecko species from arid regions with relatively cool nights. The scarcity of information and the differences in methods and species makes comparison of the data directly to that of _H. frenatus_ difficult. However, these data, combined with the results presented for _H. frenatus_, allow some generalizations and conclusions to be made about nocturnal gecko thermal relations.

Nocturnal geckos usually have a low mean activity temperature, a wide activity range, and a great deal of variation around the mean. Body temperatures are closely correlated with air temperatures, but more closely with substrate temperatures. Body temperatures are usually slightly higher than environmental temperatures because of limited nocturnal thermoregulatory behavior.

Although commonly used, the term "mean preferred temperature" should not be used in nocturnal gecko thermal ecology because of the wide variation discussed above, and because temporal differences in preferred temperatures are reported (Bustard, 1967a). Optimum temperatures for nocturnal foraging are well below the optimum temperatures maintained in their diurnal retreats which are presumably conducive to digestive processes. The limited thermoregulatory ability of foraging geckos also indicates that it is not what the animal prefers, but what the environment provides, that is important to the gecko. The term "mean activity temperature" is substituted for "mean preferred temperature" because it seems to fit the unique thermal ecology of geckos.

Periodicity

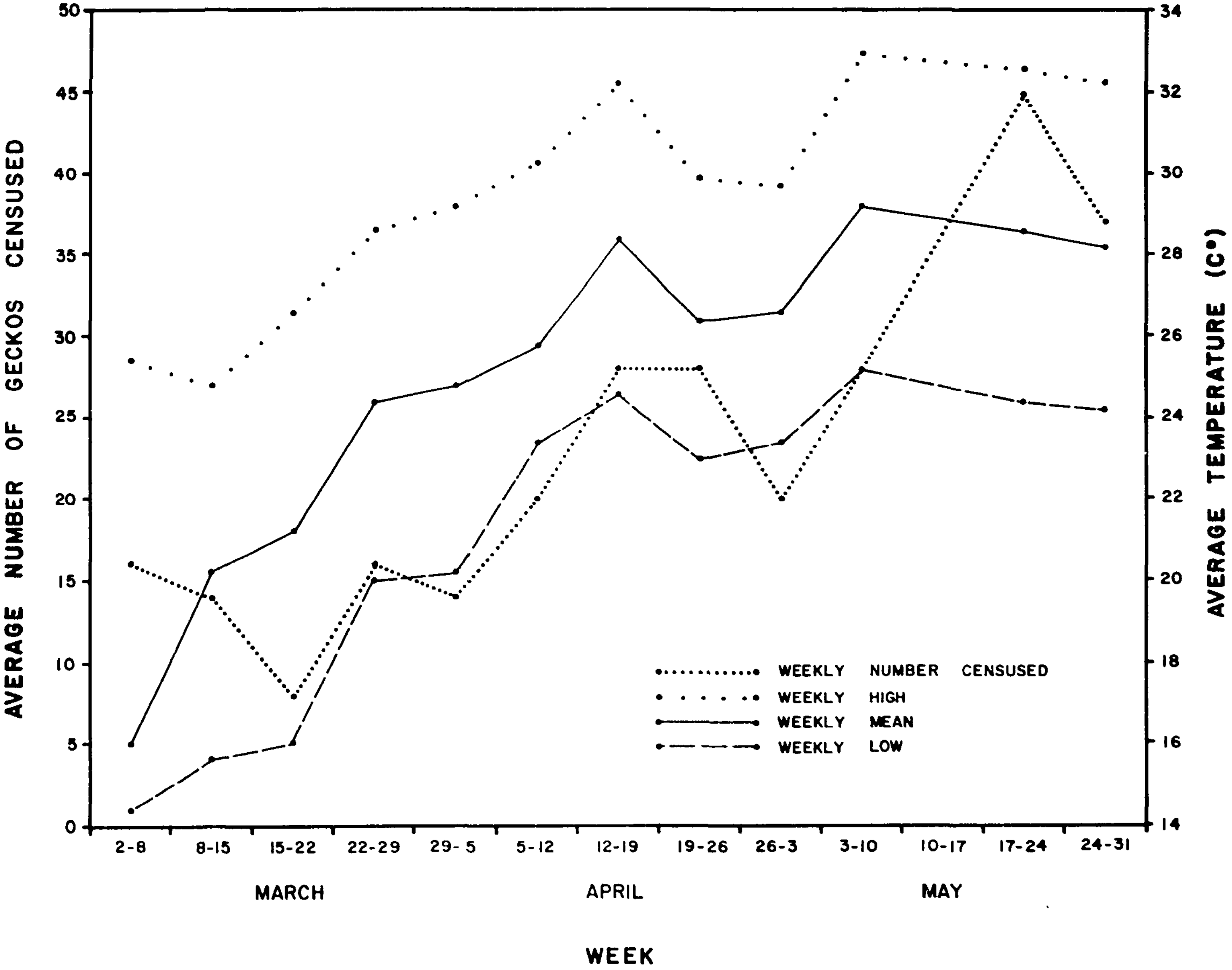
Populations have complex widespread seasonal rhythms and many periodicities associated with their diel cycle. These population periodicities and rhythms are controlled by both environmental and physiological rhythms. An attempt was made to determine monthly and daily activity cycles in *H. frenatus*, and investigate possible environmental determinants of these cycles.

Annual and monthly.--Annual activity could not be accurately resolved because of the short duration of the study, but some information was obtained from conversations with local people. It was established that active geckos can be found in every month, but activity in December, January, and February is restricted to warm days. Active geckos are said to be few in number during November, December, January and February, with numbers increasing to a high in May, June and July. Annual activity is probably largely controlled by temperature because the months of low gecko numbers are coolest and vice versa.

Activity changes over the three month study period were estimated by counts of geckos on the Main Building study area. The census was performed over a prescribed route at 10 PM on nearly every other night. The average daily number of _H_. _frenatus_ censused was calculated for each week of the study. Fig. 11 plots these data with average weekly temperature data. Numbers of active geckos increased over the study period from 16 for the first week to 37 for the last. The increase was not perfectly linear but had periods of deceleration and acceleration. The lowest weekly average, of eight, was obtained for the second week (3/8-3/15), while the highest average number of 45 was obtained for the next to last week (5/17-5/24).

Temperature is an obvious choice as an environmental determinant for monthly changes in gecko numbers, because it is known to be a controlling factor for many diurnal lizards (Blair, 1960; Tinkle, 1967). Three measures of average weekly temperature are plotted in Fig. 11. The degree of correlation between all three weekly temperature averages and the average weekly number of geckos censused

Fig. 11. Average weekly number of *Hemidactylus frenatus* at daily 10 PM census compared to average weekly temperature data. Ciudad Valles, S.L.P., Mexico, March-May 1969.


AVERAGE NUMBER OF GECKOS CENSUSED
AVERAGE TEMPERATURE (C°)
0
5
10
15
20
25
30
35
40
45
50
14
16
18
20
22
24
26
28
30
32
34
WEEKLY NUMBER CENSUSED
WEEKLY HIGH
WEEKLY MEAN
WEEKLY LOW
2-8
8-15
15-22
22-29
29- 5
5-12
12-19
19-26
26-3
3-10
10-17
17-24
24-31
MARCH
APRIL
MAY
WEEK

is quite close. As temperatures rise the number of geckos counted usually increases, and if temperatures suffer a short decline, the number of geckos censused also drops. A drop in temperature apparently does not act immediately upon gecko activity, but is felt after a short delay.

The degree of correlation, between the average weekly low, and average weekly high temperatures, and the numbers of geckos censused, was determined by calculating the product moment correlation coefficients. The r-values for average weekly high and low temperatures were 0.6695 and 0.5427 respectively. The probability of the correlation was less than 0.01 in both cases, indicating a high correlation.

A visual examination of the correlation coefficients indicates that there is a higher degree of correlation between gecko activity, and the average weekly high, than between activity, and the average weekly low. A test of homogeneity for the two correlation coefficients was nonsignificant so, on statistical terms, the hypothesis that the two r-values differ must be rejected.

High and low daily temperatures generally occur in the afternoon and early morning hours respectively (Fig. 3). The average weekly low is really an average taken during hours of gecko activity while the average high occurs when geckos are in their diurnal retreats. The closer correlation between high temperatures and gecko activity indicates that the temperature during nocturnal hours is not as good a determinant of gecko activity as temperatures during diurnal hours. This was graphically illustrated during two days early in the study. On 4 March the lowest diurnal high temperature was recorded (17.8 C at 4:00 PM) and the nocturnal low was 13.9 C (at 5:00 AM). Four geckos were censused on this night. The lowest nocturnal temperature occurred on 18 March (10.5 C at 5:30 AM). The diurnal high for 18 March was 26.1 C (at 3:30 PM) and 11 geckos were counted. Although other factors no doubt play a part, it appears that diurnal high temperatures are important in determining gecko activity.

The reasons for this apparent relationship between diurnal temperatures and gecko activity appear to be related to physiological processes and body temperature. It was pointed out, in the section on thermal ecology, that geckos generally have higher body temperatures in their diurnal retreats than they do during nocturnal foraging. It has been suggested by Bustard (1967a) that high diurnal temperatures are optimum for digestive processes. If diurnal temperatures are low, digestive processes may be greatly slowed, or cease entirely. This might act to reduce the stimulus for nocturnal foraging and result in fewer active geckos. High diurnal temperatures aid digestion which might stimulate movement and nocturnal activity.

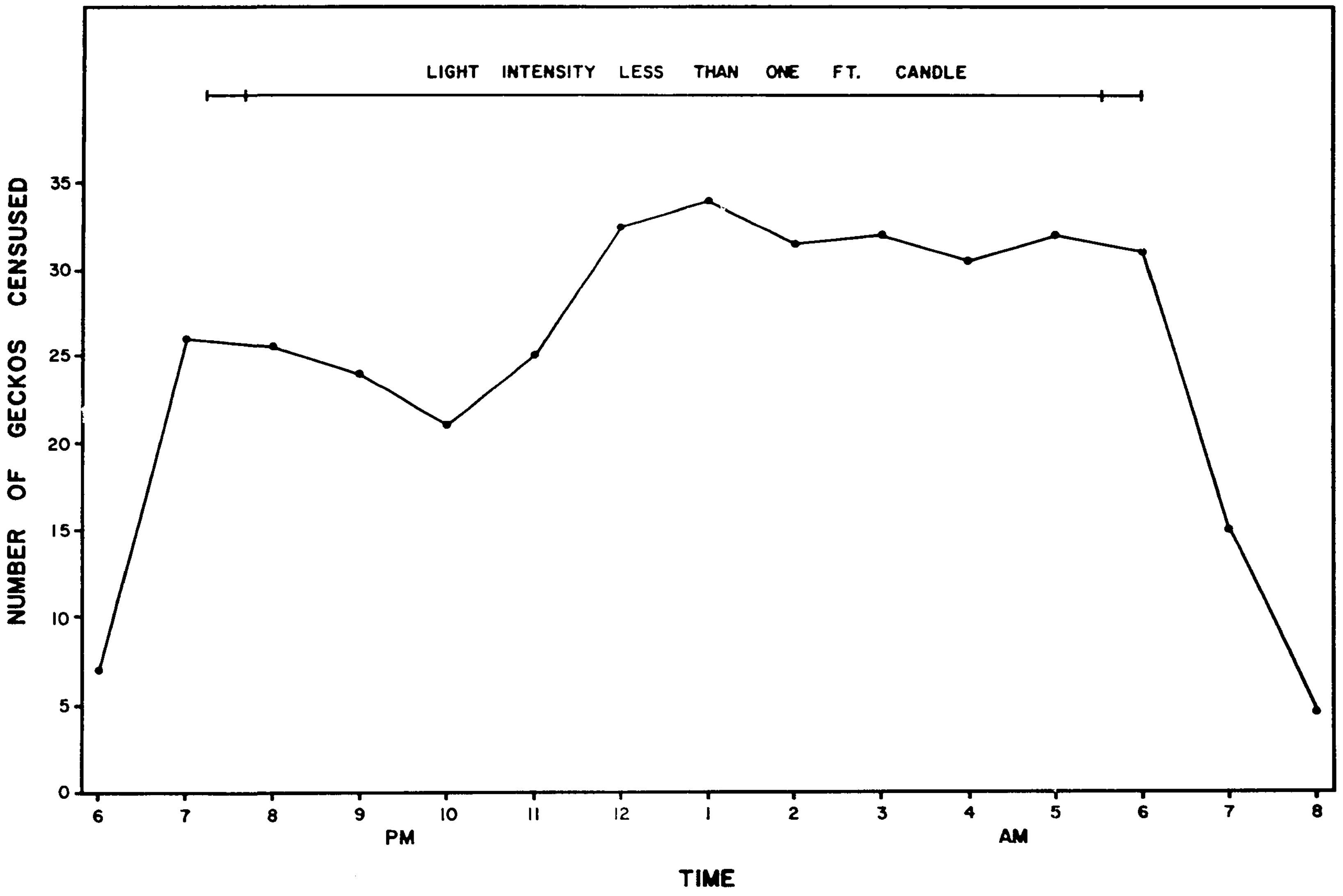
Annual and monthly activity cycles for nocturnal geckos have been reported in the literature, and appear to be related to environmental temperatures (Bustard, 1968a, b). However, no quantitative work has been reported with nocturnal tropical geckos.

Diel.--The 24 hour activity cycle was estimated by hourly counts over the Main Building porch census area. One night in March, two in April, and two in May were chosen for study. Average hourly numbers of H. frenatus for the five nights are shown in Fig. 12. Gecko activity increased rapidly from 6:00 to 7:00 PM and then dropped slightly until 10:00 PM when a secondary increase raised the numbers to a high at 1:00 AM (34). Gecko activity remained high from 1:00 to 6:00 AM when it dropped rapidly until 8:00 AM. During the daylight hours geckos remained hidden in cracks and crevices in the walls and ceilings of the hotel buildings.

The graph of gecko numbers does not go to zero because of the variation in time of emergence and retreat. A few animals came out of their diurnal retreats early and a few could always be found out after dawn. These individuals were always in regions with low light intensity near cracks or crevices. From 10:00 AM until 4:00 PM geckos were rarely seen, except on very dark days, or in the interior of the buildings.

The most probable environmental factor responsible for initiation and cessation of nocturnal activity is

Fig. 12. Average hourly census of *Hemidactylus frenatus* and hours of light intensity less than one foot candle for five nights, Ciudad Valles, S.L.P., Mexico, March-May 1969. Vertical lines at ends of horizontal light intensity line indicate the seasonal range of variation in hours of light intensity less than one foot candle.



LIGHT INTENSITY LESS THAN ONE FT. CANDLE
NUMBER OF GECKOS CENSUSED
0
5
10
15
20
25
30
35
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
PM
AM
TIME

light. Other factors, such as temperature and humidity, change only slightly and slowly at the critical hours at dawn and dusk (Fig. 3), and probably play no part in determination of the limits of the activity period.

Fig. 12 shows hours of light intensity less than one foot candle for the five census nights. Gecko activity began before dusk, and increased rapidly at dusk, remaining high until slightly after dawn. The initiation of activity before dusk, and its maintenance slightly after dawn, is probably due largely to peculiar characteristics of the census area. The lizards on the Main Building porch were under cover, where light intensity was lower, than where intensity measurements were made. Although no quantitative data were recorded, geckos in more open habitats seemed to emerge later and to retreat earlier than those on the census area.

The reaction of _H. frenatus_ to light is not a simple consistent photonegative response as is suggested by the previous statements. The animals seem to alter their reaction to light from a photonegative to a photopositive one. Geckos avoid sunlight and attempt to escape from a flashlight beam; however, numerous geckos were found in fairly well lighted regions of the hotel, and were even found feeding inside the fixtures of lighted porch lamps. The same individuals that would run from a flashlight beam were often caught, an hour or so later, inside a lighted porch light. It appears that some sort of habituation allows the geckos to enjoy the advantages of good vision, warmth and abundant food provided by the porch lamps. Much more quantitative information is needed concerning short-term photic responses in these geckos.

Although light determines the limits of the activity period, other environmental factors such as rain, wind, and human activity have secondary effects on gecko activity. Human activity was generally high on the census area from 9:00 to 11:00 PM due to arriving travelers and people going to and from late evening meals. By 11:00 PM human activity had usually declined, and remained low until morning. The level of human activity might be responsible for the drop in gecko numbers at the 10:00 PM census and the high level of gecko activity after 11:00 PM (Fig. 12). Wind and rain appeared to adversely affect gecko numbers. On 7 April a strong thunder storm struck at approximately 11:00 PM and heavy wind and rains lasted until 1:00 AM. The porch census taken at 9:30 PM was 24 but after the storm the porch count was only eight. In less protected areas there was no gecko activity. The reasons for this reduced activity are unknown, but lowered temperatures due to the wind and rain might be an important factor.

In summary, long term periodicities in _H. frenatus_ were probably largely controlled by temperature. Gecko activity increased over the study period and the increase was closely associated with rising temperatures. There is a greater correlation between the number of geckos active, and diurnal temperature, than between activity and nocturnal temperature. The diel rhythm showed that *H. frenatus* was almost exclusively nocturnal, and the environmental determinate for initiation and cessation of activity was light. Nocturnal activity was reduced by factors such as human activity, wind, rain, and low temperature.

A number of authors have discussed the diel cycle of nocturnal geckos in a general sense (Bustard, 1968a,b; Church and Chun-Sim, 1961; Heatwole, 1966; Rose and Barbour, 1968) but quantitative work has been infrequent. King (1959) determined the approximate nocturnal activity of *Hemidactylus turcicus* in Florida. This activity was found to be greatest at about 9:00 PM and then decreased until all geckos had disappeared shortly before sunrise. Park (1938) worked on the activity cycle of a species of *Thecadactylus* is a Panamanian rain forest. Activity in this species reached its peak shortly after sunset and then decreased until dawn, with a short increase in the early morning hours. Bustard (1967a) studied free-living and captive *Gehyra variegata* in Australia, and determined that the geckos had a peak activity in the hours immediately following sunset, which subsequently dropped off to a low at dawn. The above authors seem to agree that light is the environmental factor controlling the initiation and cessation of the activity period. However, temperature is suggested as a factor which determines changes in activity after dark.

The differences in nocturnal activity patterns between *H. frenatus* and other geckos studied are probably due to environmental differences. *Gehyra variegata* occurs in a semi-arid region with rapid reradiation and relatively cool nocturnal temperatures. Optimum temperatures occur shortly after dusk, followed by less favorable thermal conditions until dawn. Bustard (1967a) states that these temperature factors are directly responsible for the pattern of nocturanl activity in *G. variegata*. The same situation may exist in the case of *H. turcicus* in Florida; low early morning temperatures resulting in lessened gecko activity during these hours. Although tropical, *Thecadactylus* is found in a quite different habitat from *H. frenatus*, and consequently the differences in nocturnal activity patterns are probably a result of the numerous ecological differences between the two species.

Habitat preference

The way in which an animal locates and or positions itself in the habitat is a complicated process. Responses to multiple environmental factors tend to keep animals in their so-called "preferred habitats". The present study describes some aspects of habitat preference in *H. frenatus*.

Distribution.--*H. frenatus* was abundant on the grounds of the Hotel Valles and in houses and stores in the northeast part of the town. Although only a cursory investigation of its urban distribution was made, it appeared that the geckos were most abundant in well lighted areas, especially in the stores along the main highway.

Within the hotel grounds the geckos could be found on nearly every structure, including the stone walls around the periphery of the property. They were particularly numerous on the Main Building, the Doña María, and the home of Thomas Osuna (Fig. 4). Geckos were also observed on small isolated structures such as garden lamp posts and the swimming pool diving platform. Geckos occurred on some trees in the garden, but only small numbers were observed. Trees harboring geckos were usually large, and were located on the periphery of the garden, or near buildings.

On any individual building, H. frenatus could be found in and on all parts of the structure. Lizards occurred on first and second story exterior walls, and on walls and ceilings of rooms and porches. On a given building abundance varied from place to place with large accumulations in some areas.

In the Main Building geckos were particularly abundant in a number of places. The palm thatch roof of the dining room provided shelter for a large number of geckos. After dark these animals could be seen feeding near lights on the walls of the dining room. Large numbers were also found on the front porch study area. In daylight hours these animals remained within the numerous cracks and crannies in the ceilings and walls. At dusk they emerged to feed around the porch lights. Smaller accumulations of geckos occurred on certain well lighted walls that had adequate places of refuge nearby.

Doña María geckos were more evenly distributed than the Main Building animals, but a large accumulation was found on the upper west porch. This region was well lighted, had a high ceiling, and was in a quiet part of the building. Smaller concentrations of Doña María animals were also found near porch lights, and in the corners of the porches. These accumulations were generally associated with a crack or hole within which the geckos could seek shelter.

Perch site.--Table 10 shows perch heights of *H. frenatus* by sex and building. No significant sexual differences in perch heights were found on either building. The highest perch site was 4.9 m and the lowest 0.6 m. Main Building perch sites averaged 2.75±0.82 m above floor level while Doña María perch sites averaged 3.4±0.725 m. The means of the two buildings are significantly different at the $P < .001$ level. Although the ranges were fairly large the variation between individuals on both buildings was small. In all cases the means were much closer to the

Table 10. Perch height* (m) by sex and building of *Hemidactylus frenatus* from Ciudad Valles, S.L.P., Mexico, March - May 1969.

Building	Sex	Number	Mean	Range	Standard Deviation
Main	Male	98	2.8	0.6-3.7	± 0.76
	Female	124	2.7	0.6-3.7	± 0.87
	Total	222	2.75	0.6-3.7	± 0.82
Doña María	Male	53	3.3	1.8-4.9	± 0.70
	Female	66	3.5	0.9-4.9	± 0.75
	Total	119	3.4	0.9-4.9	± 0.725

*Estimated to the nearest 1/10 m from floor level.

upper limits of the ranges than to the lower limits. This indicates that H. frenatus is generally found high on walls or ceilings and is only rarely found near floor level.

Building differences in mean perch height seem to be closely related to differences in ceiling height. The ceiling on the Main Building porch varies from 3.7 m to 2.7 m in height while the Doña María ceiling varies from 4.9 m to 3.7 m. The geckos apparently prefer perch sites very near the ceilings and are found at greater heights when these heights are available. This was particularly noticeable on the upper west porch of the Doña María. The ceiling on this porch was a meter higher than adjacent areas, and a greater number of geckos were found in this region.

There are three apparent advantages of high perch sites. First, the geckos are out of reach of most potential predators, including humans. Second, the microclimate near the ceiling has certain advantages, such as shelter from wind and rain, and higher temperatures (1 or 2 C) than floor level temperatures. Third, many insects enter the porches in response to light, and land high on ceilings and walls, providing an abundant food supply for the geckos.

The Main Building porch was chosen for study of substrate preference because it provided the widest variety of substrate types. Numbers of geckos on various substrate types are enumerated in Table 11. The largest number recorded were on wood (83) with the smallest number occurring on metal (18). The number of geckos recorded on the various substrate types can be compared with the area covered by the substrate type to determine if geckos were merely distributed in proportion to available area. Wood covered approximately 167 m^2, and 83 lizards were recorded on this substrate type. Stone covered 346.8 m^2, and only 24 geckos were noted on this type of substrate. Glass made up only 3.7 m^2, and yet 36 animals were recorded on this limited area. Thus it appears that the geckos tended not to be distributed in proportion to the substrate area, but showed real preferences for certain substrates.

The substrate preferences are probably due to the texture and location of the preferred substrates. Wood makes up the ceiling of the porch, and a strip 20 cm wide along the top inner wall. The wood is rough and provides excellent purchase for locomotion. The inner and outer walls of the porch are constructed of stone and are relatively smooth. Lizards were observed on the stone, but they appeared to be less active, and occasionally fell from this surface. The wood substrate, being at a greater height, also has the advantages of warmth, food and protection discussed for high perch sites.

The glass and metal substrates cover a small area and

Table 11. Number of *Hemidactylus frenatus* on various substrate types and area covered by substrate types,* Ciudad Valles, S.L.P., Mexico, March - May 1969.

Substrate Type	Approximate Area Covered by Substrate Type (m^2)	Percent of Total Area	Number of Geckos	Percent of Total Number
Wood	167.0	32.1	83	52
Stone	346.8	67.0	24	15
Glass	3.7	0.7	36	22
Metal	0.9	0.2	18	11
Total	518.4	100.0	161	100

* Main Building porch study area

Table 12. Number of male and female *Hemidactylus frenatus* on vertical and horizontal surfaces, Ciudad Valles, S.L.P., Mexico, March - May 1969.

	Vertical	Horizontal
Male	101	51
Female	144	56
Total	245	107

are restricted largely to porch light fixtures. The advantages of food and warmth provided by the lights make up for the disadvantages of smooth surface and small area.

Orientation of perch site substrate was recorded for 352 captures from the Main Building and Doña María (Table 12). Sexual differences in orientation of perch site were found to be non-significant using a Chi-square test of independence. A decided preference for vertical substrates appeared to be present, with 245 of 352 animals being recorded on vertical surfaces. If no preference for orientation of substrate existed, and the areas of the two surfaces were similar, we would expect equal numbers to be recorded for vertical and horizontal. A Chi-square goodness of fit test was used to test this 50:50 hypothesis, and a highly significant deviation from expected was obtained ($P < .005$). The areas of vertical (walls) and horizontal (ceilings) surfaces on the study areas are approximately equal. The data on perch heights showed that animals were found largely within a meter of the ceiling. Thus the utilized wall area was much smaller than the area of the ceiling, and yet the geckos show a definite preference for vertical surfaces.

The apparent reason for a vertical substrate preference in H. frenatus is that such a surface offers better purchase. On a vertical surface the geckos are able to utilize the friction of their bodies against the substrate, as well as their modified digits, to keep them from slipping or falling. On a ceiling the only friction and grip is provided by the modified digits. Many geckos were observed on ceilings, and could move about on such a surface, but it appeared that these geckos were less active, and if chased, were more likely to fall. It is reasonable to assume that the geckos prefer the vertical (wall) substrate over the horizontal (ceiling) substrate because much less energy is required to cling to, and move about on, such a surface.

The orientation of male and female geckos on vertical surfaces is enumerated in Table 13. The numbers of stationary animals in three positions were noted. A Chi-square test of independence was used to compare the frequencies of the two sexes in the three categories of orientation. A non-significant difference was found between the orientation of the sexes. The majority of animals were observed in a horizontal position (169) while nearly equal numbers were recorded with head up (23) and head down (24).

The significance of this preponderance of horizontal orientation is unknown, but two suggestions can be made. First, it is possible that the horizontal position provides some sort of advantage in clinging to the vertical substrate. Second, the horizontal position allows the animals to situate themselves in the junction of the wall and ceiling where they can enjoy the advantages of warmth, height and concealment.

Table 13. Orientation of male and female *Hemidactylus frenatus* on vertical surfaces. Ciudad Valles, S.L.P., Mexico, March - May 1969.

	Head Up	Head Down	Horizontal
Male	11	11	60
Female	12	13	109
Total	23	24	169

In summary, *H. frenatus* prefer large complex structures with some artificial light. Concentrations of animals occur in areas with adequate places of refuge, some artificial light, and low levels of human activity. Perch sites are generally high, on wood, and vertical. Height and vertical orientation are the most important factors. Orientation on vertical substrates is largely horizontal.

The literature concerned with gecko habitat preference deals primarily with diurnal geckos, but some work has been done on nocturnal geckos similar to *H. frenatus*. King (1959) and Rose and Barbour (1968) both mention that *Hemidactylus turcicus* was found on walls of buildings, and that they took shelter in cracks and crevices. Church and Chun-Sim (1961) discussed the distribution of three species of gecko in Bandung, Java and found species differences related to light and humidity. *Cosymbotus platyurus* occurred in well lighted dry areas near the center of the town, *H. frenatus* in well lighted damp residential areas, and *Peropus mutilatus* in dark areas throughout the town. Heatwole (1966) investigated factors affecting orientation and habitat selection in several tropical geckos. Using experimental methods he found that the nocturnal *Thecadactylus rapicaudus* and *Hemidactylus brooki* were photonegative while the diurnal *Sphaerodactylus lineolatus* and *Gonatodes fuscus* were photopositive. Heatwole also discovered that *G. fuscus* preferred vertical surfaces and utilized crevices. Much more quantitative work on habitat preference must be done before meaningful interspecific comparisons can be made.

Home range, movement and territory

Home range and movement.--The area occupied by an animal throughout its life has been called home range. Studies on home range indicate the area necessary to sustain an individual, and relationships of individual home ranges can provide insight into the social structure of a population.

Home range has been defined and studied in a number of ways. In the present study, the small number of captures for individual animals, and the nature and use of the habitat by *H. frenatus* makes conventional methods of home range study difficult. The usual minimum polygon method of home range determination requires at least three captures, however such data were available for only a few animals. Also, the points of capture of individuals were generally linear, being along the junction of the wall and ceiling. This use of the habitat did not facilitate the drawing of home range areas. To avoid these problems, it was decided to use average distance between captures as an estimate of home range size.

Average distance between successive captures reflects the frequency of movement and the relative area occupied by an animal (Tinkle, 1967). Tables 14 through 17 show the average distance between captures for individual _H. frenatus_ by sex and building. The greatest distance between captures was 14.3 m, recorded for a male on the Doña María, and the smallest distance was zero, for a number of animals of both sexes on both buildings. The average distance between captures of Main Building animals was 2.7 ± 2.14 m for males and 3.9 ± 2.74 m for females. The average distance between captures for Doña María males and females was 7.2 ± 4.48 m and 3.8 ± 3.62 m. Main Building females appeared to move further than males, while on the Doña María, the opposite seemed to be the case. If we combine sexes for each building the Doña María individuals averaged a greater distance per move than Main Building animals (5.5 to 3.3 m).

The differences between the means can be tested statistically using t-tests. The average distance between captures of Main Building males is statistically different

Table 14. Average distance between captures for male *Hemidactylus* *frenatus* on the Main Building, Ciudad Valles, S.L.P., Mexico, March - May, 1969.

Individual	Avg. S-V Length (mm)	Times Moved	Avg. Distance (m) Between Captures	Number Captures
57	40	0	0	3
43	42	2	1.5	3
185	42	1	3.4	2
61	44	1	1.2	3
88	47	1	8.2	2
115	47	1	2.4	2
54	48	1	1.5	2
122	48	1	0.9	2
159	49	1	2.1	2
44	50	1	1.8	2
26	52	1	1.5	2
92	52	1	2.1	2
5	53	3	4.0	4
15	53	1	4.3	2
42	53	1	3.7	2
178	53	0	0	2
154	54	1	2.4	2
30	56	1	1.5	3
157	56	0	0	2
1	57	10	4.0	12
147	58	1	9.1	2
130	59	2	4.6	3
Average	50.6	1.5	2.7	2.7

Table 15. Average distance between captures for female *Hemidactylus frenatus* on the Main Building, Ciudad Valles, S.L.P., Mexico, March - May, 1969.

Individual	Avg. S-V Length (mm)	Times Moved	Avg. Distance (m) Between Captures	Number Captures
105	40	1	9.5	2
14	42	1	7.6	2
3	43	2	4.3	3
221	44	1	0.9	2
156	48	2	2.4	3
87	49	1	1.5	3
217	49	1	1.8	2
4	50	1	11.3	2
12	50	2	1.5	3
60	50	1	2.4	2
97	50	1	1.2	2
10	51	3	1.8	5
13	51	1	6.7	2
150	51	2	1.5	3
163	51	1	5.2	2
20	52	2	2.4	3
7	53	2	3.4	3
8	53	1	1.5	3
151	53	1	2.7	2
31	54	2	7.9	4
65	54	5	5.5	4
68	54	1	2.1	4
Average	49.6	1.5	3.9	2.8

Table 16. Average distance between captures for male *Hemidactylus frenatus* on the Doña María, Ciudad Valles, S.L.P., Mexico, March - May, 1969.

Individual	Avg. S-V Length (mm)	Times Moved	Avg. Distance (m) Between Captures	Number Captures
160	43	1	10.7	2
179	44	2	7.0	3
102	45	2	1.2	3
139	46	1	7.9	2
74	50	2	5.2	3
108	50	0	0	2
171	51	1	7.0	2
234	52	1	12.2	2
39	53	1	0.6	2
76	53	1	14.3	2
36	54	1	6.1	2
73	54	1	3.4	2
38	55	4	3.4	5
77	57	2	13.1	3
182	58	1	9.1	3
75	59	1	13.7	2
Average	51.5	1.4	7.2	2.5

Table 17. Average distance between captures for female *Hemidactylus frenatus* on the Doña María, Ciudad Valles, S.L.P., Mexico, March - May, 1969.

Individual	Avg. S-V Length (mm)	Times Moved	Avg. Distance (m) Between Captures	Number Captures
172	43	1	3.1	2
35	44	1	10.4	2
135	45	2	1.8	4
140	47	1	0.9	2
49	49	1	10.7	2
85	50	2	1.2	4
37	51	1	1.5	2
166	51	0	0	2
47	53	1	1.2	2
51	53	0	0	2
82	53	1	9.5	2
86	53	0	0	2
101	53	2	5.2	3
126	53	1	2.1	2
164	53	2	4.6	3
69	55	1	9.1	2
111	56	1	4.3	2
Average	50.7	1.0	3.8	2.9

from the average of Doña María males ($P < .01$), while the same comparison for females is non-significant. There is a significant difference between the means of the sexes on the Doña María at the $P < .05$ level. The difference between the means of the sexes on the Main Building is non-significant.

It is felt that the reasons for these differences in movement on the two buildings are related to population density and habitat differences. It was pointed out that the complex environment of the Main Building porch supports more lizards than the relatively simple Doña María habitat. The estimated density on the Main Building was over 6 times greater than that on the Doña María. The higher density on the Main Building probably serves to reduce movements due to aggressive interactions between individuals. The males are much more aggressive than the females, and thus show the effect of the high density more graphically. This results in reduced movement in Main Building males compared to Doña María males.

To determine if differences in movement were related to gecko length the individuals in Tables 14 through 17 were divided into snout-vent length groups and inter group comparisons of movement made. Table 18 compares the average distance between captures of the three size groups for each sex. Males showed an increase in average distance between captures for each increase in size class while females did not.

Table 18. Length of lizard compared to distance between captures. Data from Tables 14 through 17.

	Sample Size	Avg. S-V Length (mm)	Avg. Meters Per Move
Males	12	44.7	3.8
	13	51.6	4.5
	13	56.2	5.4
Females	13	45.6	4.3
	13	51.3	3.0
	13	53.4	4.3

Increase in movement in relation to increase in body length has been demonstrated in other lizard studies such as those by Blair (1960), Tinkle (1967), and Rand (1967). These studies also show that after females reach sexual maturity they do not increase their movements with increasing body length. The continued increase in movement with increasing size in males could be associated with increasing dominance and aggressiveness. Larger male lizards (of a species) tend to be more aggressive than small males (C.C. Carpenter personal communication). Increasing aggression with increasing size allows males to increase their sphere of influence. Females are relatively non-aggressive, and increase their movements only slightly with increase in size after reaching sexual maturity.

Although conventional home ranges could not be constructed for most animals, a reasonably accurate picture of home range size was determined for a single individual (Number 1). Number one was a male that frequented the Main Building lobby. This animal was either observed or captured 12 times from 3 March to 21 May. Number one's movements were centered around a hole in the stucco high behind the main desk. From this retreat he ranged as far as 12.0 m, but the average distance between captures for 10 moves was 4.0 m. A minimum home range was plotted for this animal by connecting the outside points of capture. The resulting nearly rectangular area was approximately

76 m^2. Cockrum (1962) has pointed out that home range size determined in this way is usually less than the actual home range size.

The average distance between captures for individual number one falls between the average distances computed for males in Tables 14 and 16. It is not known if the minimum home range for number one is representative for all males in the population, but considering the accuracy of the movement data it is probably reasonably close to an average male home range.

Published data on movements are readily available for a number of lizards, but comparisons are difficult because of differences in the techniques used to gather data. In non-gekkonids reports of average distance between captures of both sexes range from 2.1 m in Leiolopisma zelandica (Barwick, 1959) to 45 m in Cnemidophorus sexlineatus (Fitch, 1958). Home ranges for adults vary from 203 m^2 in Basiliscus vittatus (Hirth, 1963) to 1219 m^2 in Cnemidophorus tigris (Jorgenson and Tanner, 1963). Reports in the literature have shown gecko movements to be restricted to small areas. Bustard (1968a) found that Gehyra variegata moved very little, and that animals generally remained on one tree. The same was found to be true of two species of diurnal Lygodactylus studied by Greer (1967). Rose and Barbour (1968) found that individual Hemidactylus turcicus remained in rather limited areas, with a mean distance between captures of 3.7 m. Increased movement with increased size has not been previously reported in geckos, nor have home ranges been quantitatively determined.

Geckos appear to have much smaller home ranges and distances between captures than other lizards studied. Although body size may have some effect on home range and movement (smaller species with a smaller home range and vice versa), the real reason for the relatively small home ranges and distances between captures of geckos is probably the high population densities in the complex environments inhabited by many geckos. High densities and intraspecific aggression would serve to reduce movement in these populations. Work on non-gekkonid species with high population densities should also show small home ranges and movements.

Territory.--Territories and territorial behavior have been described for a number of lizards. The adaptative significance of territoriality in some lizards has been discussed by Rand (1967). Carpenter (1967) operationally defines territory as "an area that is aggressively defended against intrusion by others of the same species". An attempt was made to determine if individual H. frenatus maintain territories.

Two methods in conjunction are generally employed to demonstrate the presence of territoriality in a population of lizards. The first method utilizes observation of marked individuals to determine the existence, size, and dynamics of territories. The second method involves a capture-recapture program which is used to map home ranges and to determine to what degree they overlap. From these data the size and dynamics of territories can often be determined. The second method could not be used in _H. frenatus_ due to the reasons stated in the previous section, and the results below were obtained solely by observation.

It was noted that adult females were highly tolerant of other geckos of both sexes. Females were often observed in groups of four or more, and with individuals only inches apart. Adult males, on the other hand, were tolerant of females and juveniles, but antagonistic toward other adult males. Aggressive interactions were observed between adult males, and males were rarely seen at the same time and place.

Sexual composition was determined for contiguous aggregations of geckos that could be collected over a short period of time. Two groups were collected in this manner. The first consisted of 13 animals which inhabited the upper stairwell of the Doña María, and the second was a 12 animal group on the east end of the Main Building porch. The dimensions of the areas frequented by each of these groups were approximately two by three meters. The Doña María aggregation was collected on 29 March, and consisted of two adult males, one subadult male (under 50 mm snout-vent), seven adult females, and three subadult females (under 45 mm snout-vent). The Main Building group, collected on 4 April, was composed of one adult male, two subadult males, 8 adult females, and one subadult female. These groups were probably atypical because of their relatively large size, but they corroborate the observations that adult males are more tolerant of females than they are of other adult males.

The Doña María group was particularly interesting to observe because it contained two adult males. The two males were often active at the same time, but they seemed to avoid each other. If one male was at one end of the stairwell ceiling, the other male would be found at the other end. The females and subadults moved freely over the ceiling, being associated first with one male and then with the other. The males also moved and exchanged positions on the ceiling, but they always remained at least a meter apart. No aggressive interactions were observed between the adult males, although both males engaged in low intensity aggressive encounters with subadult males.

Many adult males were marked and subsequently found to frequent particular areas of the buildings. Early in the study it was noticed that more than one adult male was often captured in the same area, and often in exactly the same location. Accurate long term records of this phenomenon were impossible to keep because of difficulties in regular capture and marking, but some observations were made. It was noticed that males alternated in the use of an area. This was not a regular nightly rotation of males, but was a highly irregular alternation. An individual male might be observed in an area for five nights, and then be replaced for a night by another male. Or an animal might be observed for a week and then be replaced for one or two nights by another male. In all cases, one male was commonly found in a particular area, and was only replaced for a short time, at infrequent intervals, by another male. This type of behavior usually involved two males, but on at least one occasion three adult males alternated.

An adult male (no. 76) that commonly frequented the upstairs northwest corner of the Doña María was replaced by another male on 12 April. On this date, number 76 was captured in the downstairs northwest corner of the Doña María, replacing a male that commonly frequented this location. On 13 April the males were back in their usual locations. Male number 76 was displaced approximately 6 m vertically during the move. This was the only instance when the movement of a replaced male was followed, and it is not known if this is a common occurrence.

How the replacement is accomplished is not known, but it is possible that the occupancy of an area is determined by the male that gets there first. A male which has a nearby retreat will generally be found on a particular area, but if he is tardy in emerging another male may take over his area. This could force the replaced animal into an unfavorable area or into another male's area.

Many adult males did not appear to undergo this rotation, and were always found in a specific location. Two adult males that frequented opposite ends of a wall on the Main Building stairwell could always be found in this area. These animals were observed a number of times and appeared to have well defined territories. Each individual's territory was centered around a crack in the plaster-board near the ceiling. These cracks were in opposite corners of the wall, about 9 m apart. Associated with each male was a number of females and subadults. All these animals fed around lights on the stairwell wall. The females and subadults of each group intermingled extensively during foraging, but marked animals were observed to return to their own side after feeding. The adult males also foraged on the wall but each remained on his own side and never went more than a half a meter past the center of the wall. The resulting territories had diameters of about 4 m. On the night of 15 May the two males were foraging near the center of the wall at the same time, and a high intensity aggressive interaction ensued. At the end of the encounter, both males returned to their respective ends of the wall.

Territoriality in gekkonid lizards has been reported for numerous species. Most of these reports have been based solely on observations, such as the remark of Church and Chum-Sim (1961) that individual *H. frenatus* "tend to exert territorial rights over their own particular areas". Quantitative work on territoriality has been done by Bustard (1968a,b) on two species of Australian geckos. He found that males defended territories which often contained two or more females. Greer (1967) obtained quantitative data on territoriality in two species of African *Lygodactylus* geckos. The males of these diurnal geckos were found to be highly territorial, while females were gregarious and found within male territories.

The observations in the present study, and the literature both demonstrate that territoriality is a strong force in gecko populations. In *H. frenatus* more than one type of territoriality seems to be present. Some males exhibit classic territoriality and defend a given area from conspecific males. Other individuals defend small areas around themselves. These territories are dynamic and move with the individual. The factors that determine the type of territoriality exhibited by an adult male *H. frenatus* are unknown. Other gecko species seem to demonstrate the classic type of territoriality, with one male defending a static area. The reasons for these intraspecies and species differences in territorial behavior are not known.

Breeding structure

The breeding structure of the Ciudad Valles gecko population is suggested by the above data. The adult sex ratio is slightly biased in favor of females. Male *H. frenatus* are territorial and defend their territories against other males. Females are not territorial and are often found in groups within male territories.

Observations made on marked groups of lizards demonstrated that male *H. frenatus* are polygamous. A group of marked geckos on the upper west porch of the Doña María was under periodic observation for two months. This group consisted of one large male, two subadult males, four adult females, and two subadult females. The large male was observed to copulate or attempt copulation with all females in this group. On the night of 13 April the male successfully copulated with two females within a two hour period. The subadult males did not exhibit sexual behavior. Other groups showed similar sexual composition and behavior. The type of relationship exhibited by these groups of animals can be called a limited polygamous breeding structure because the territorial male had a large but limited number of potential mates. The advantages of such a system are discussed in the section on sex ratios.

There is little information in the literature dealing with breeding structure in lizard populations, but detailed studies that have been made indicate that facultative monogamy is common (Blair, 1960; Harris, 1964; Tinkle, 1967). Work on geckos has also been limited, but polygamy is indicated by Bustard (1968a,b) who reported that the nocturnal Gehyra and Heteronotia males share their territories with one, and often more than one, female. Greer (1967) stated that diurnal Lygodactylus males share their territories with two or three females.

Breeding cycle

The breeding cycles of lizards in temperate areas are known to be governed by external stimuli. Temperature is usually considered the most important, with light, rainfall and food supply being of lesser importance. In the tropics the factors mentioned above are nearly uniform throughout the year. Such conditions should result in breeding cycles that differ from those in temperate areas.

The breeding cycle of H. frenatus can be determined from the literature and from limited field observations. Church (1962) reported that H. frenatus reproduce throughout the year in Bandung, Java. He stated that this reproductive constancy was apparently brought about by unchanging climatic factors, day length and food supply. In Ciudad Valles geckos seem to be reproductively active whenever climatic conditions are favorable. During the three month field study all stages of the breeding cycle were observed; mating animals, gravid females and hatchlings. During a short visit in August all stages were again observed.

Two hard shelled eggs are laid, one from each oviduct (Church, 1962). Three clutches of two eggs each were laid by captive animals between 4 April and 8 April, but none were hatched. The eggs averaged 8 by 11 mm in diameter at laying.

The estimated breeding cycle for H. frenatus is as follows: in February animals emerge from their winter retreats and territoriality, male aggression and mating begin. This activity continues, with egg laying and hatching of young, until cold weather returns in November or December. Fertilization to hatching requires about 8 weeks (Church, 1962), so in the approximately nine month activity period at least three broods per female would be possible.

Studies of reproductive cycles in tropical geckos have been few in number. Mahendra (1936) states that the reproductive cycle of Hemidactylus flaviridis depends upon climatic conditions and breeding may continue from February to October. Rose and Barbour (1968) studied H. turcicus in New Orleans, and found that the reproductive season extended from April to August, and that two or three clutches could be produced per season.

These studies, and the present work, indicate that the reproductive cycle and number of clutches in tropical geckos is closely correlated with climatic conditions. If conditions are suitable for activity, the animals breed and reproduce.

Feeding habits

No attempt was made to accurately determine food utilization by H. frenatus, but general observations were made on food types and feeding behavior.

H. frenatus spent a great deal of time feeding, and appeared to be an opportunistic feeder. Geckos were observed feeding on small dipterous insects, moths, leafhoppers, damsel flies, roaches, and beetles. The major food items were mosquitoes and midges which occurred in large numbers around the lights. Geckos avoided feeding on certain types of insects, thereby demonstrating prey selectivity.

On three occasions counts were made of insects ingested by individuals in a five minute period. The counts averaged 22 insects per five minutes. One of these animals (an adult male) consumed 33 small dipterous insects, two leafhoppers, and a small moth in a five minute period. These feeding rates did not appear in the least unusual for foraging animals. It is obvious that feeding cannot continue at this rate for the entire night. Feeding activity seemed to be high for about two hours after sundown, and then dropped off to its lowest level in the hours before dawn.

One factor which is used by lizards to determine the type of food they will consume is the size of the food item. Generally a rather limited size range of food items exists for a particular type of lizard (Oliver, 1955). H. frenatus is unusual in having an extremely wide size range of possible food items. Not only did they feed on mosquitos, but a number of instances were recorded of geckos attacking very large insects. An adult male was observed on the wall of the Main Building porch in a struggle with a 6 cm long oriental cockroach. The roach escaped. On another occasion a Doña María female stalked and grasped a very large moth (20 cm wing span), which took flight knocking the gecko to the floor. It is not known if the geckos ever succeeded in subduing such large prey, but this ludicrous behavior was common.

The insectivorous nature of house geckos makes them of use to humanity. Miyamoto (1930), in a study of *Gecko japonicus* and *Hemidactylus bowringii*, found that these lizards consume as many as 40 to 50 mosquitos daily. Limited observations on food habits of *H. frenatus* indicate that these animals might also be a very effective control on insect pests. The numbers of mosquitoes eaten by the entire Ciudad Valles population was probably quite large. The owner of the Hotel Valles (Tomas Osuna) was quite convinced that the geckos were a major reason for the low level of mosquito activity at the hotel. More work should be done to determine if these lizards are an effective biological control for insect pests.

Vision played a prominent role during feeding by *H. frenatus*, and is highly developed. Geckos were seen to orient toward, and approach, a mosquito landing 3 m away.

Animals were also observed watching the flights of other small insects which were quickly and directly approached when they landed.

Two types of approach behavior to potential food items were observed, dependent upon the size of the food item. The first, and most common method, was utilized on small prey and consisted of a rapid approach and a quick snap. The second method was used on larger prey species and was more deliberate. The gecko approached rapidly at first, then slowed as it neared the prey. The last 10 cm were traversed a step at a time, much like a cat stalking a bird. When within 3 or 4 cm a sudden snap was made. The lizard then would make violent wiping motions with its head, rubbing the prey insect roughly over the substrate. The insect was slowly swallowed with the aid of chewing movements. A vocalization occasionally (15 observations) followed large prey feeding.

The literature dealing with food and feeding habits of geckos is fairly extensive, but not very informative because of opportunistic feeding behavior, and variability of habitats and habits. Some published observations of gecko food habits are interesting because of their unusual nature. Church (1962) reported that *Peropus mutilatus* and *H. frenatus* can feed on boiled rice, small pieces of fish, ground meat, sugar, honey, bread crumbs, and even milk. Greer (1967) stated that *Lygodactylus* geckos lick the viscous amber colored exudate of _Acacia_ trees, and will also lick jams and jellies, with apricot being their favorite flavor. No such epicurean tastes were noticed in the Ciudad Valles geckos.

Locomotion

The remarkable ability of geckos to move with ease on walls and ceilings has interested naturalists for some time. Many authors have speculated on the mechanisms that make these feats possible. The work by Mahendra (1941), and recent studies aided by the electron microscope (Gennaro, 1969) have finally resolved the problem. The mechanism is apparently a combination of gripping by the claws, and gripping and suction by the subdigital lamellae. Observations of some factors involved in the locomotor behavior of _H. frenatus_ are discussed below.

The locomotor movements of the limbs of geckos on a wall or ceiling are similar to the movements of a quadruped walking dorsal side up on a horizontal surface. If we begin with the right forefoot, the next leg to lift is always the hindfoot on the left side; this is followed by the left forefoot, and this in turn by the right hindfoot, after this the order is repeated. But postural differences between gecko locomotion and the locomotion of most other quadrupeds are marked. The sprawling posture of primitive land vertebrates has been modified by most land animals to raise the body off the ground. Most lizards lift their bodies from the substrate during locomotor movements, and as the speed of locomotion increases the lifting of the body becomes more pronounced. Many geckos have retained, or secondarily adopted, the sprawling posture of primitive land vertebrates, the body is kept close to the substrate even during high speed locomotor movements. The limbs extend out to the side of the body and much of their lower surface rests on the substrate. Associated with this sprawling posture are sinuous movements of the body during locomotion. This posture and movement is utilized on both walls and ceilings.

These locomotor characteristics seem to serve to increase frictional contact with the substrate. The frictional contact and the sinuous movements aid the animal in clinging to vertical surfaces. It is also possible that it provides some advantage in clinging upside down on ceilings.

The agility of the animals is remarkable. _H. frenatus_ can move both forward and backward on walls and ceilings with apparent ease, but both speed of movement and agility are less on ceilings than on walls. Harried animals are much more likely to lose their grip and fall when on ceilings.

The nature of the substrate affects the locomotor abilities of the lizards. Locomotion is facilitated by rough surfaces such as stucco and wood. _H. frenatus_ can move on smooth vertical glass surfaces, but will often slip downward if they remain stationary. The animals cannot cling upside down on a horizontal glass surface. A gecko's ability to stick to a surface is greatly reduced if the surface is wet. Purchase can be retained on very rough wet surfaces, but smooth wet surfaces cannot be climbed.

Falls due to natural causes were uncommon but some were observed. Two falls attributable to aggressive encounters between males were noted. In each case one male was attacked, lost his grip, and fell. In both cases the fallen animal quickly regained the wall. Six falls were seen during feeding activities, one of which was described previously in the section on feeding. The falls either involved large prey items, which in attempting to escape dislodged the lizard (2 cases), or an overly enthusiastic rush and loss of grip by the gecko (4 cases). In all cases the lizards regained the wall and seemed no worse for the experience.

Eliminative behavior

Eliminative behavior was observed in both free-living and captive animals. Defecation in *H. frenatus* commonly occurred directly following emergence from diurnal retreats, and an individual generally had a favored spot for eliminative behavior close to its place of refuge.

Defecation behavior in these geckos was similar to that found in iguanid lizards, but two slightly different types of behavior were observed depending upon orientation of the substrate. On ceilings, the hindlegs were spread and the hind quarters were slightly raised. The tail was shifted down and arched forward over the back of the lizard as elimination occurred (Fig. 13A). On vertical surfaces (walls) the behavior was similar, except that the tail was arched and shifted slightly to the side as defecation occurred (Fig. 13B). On three occasions a faint call was uttered while the gecko was defecating. The significance of this call is not known, but further description and discussion will be found in Chapter V. Post-eliminative behavior was occasionally observed, and consisted of a wiping motion of the cloacal region over the substrate.

Escape behavior

No quantitative data were obtained on escape behavior, and the observations mentioned below were largely from the reaction of lizards to humans. Escape in *H. frenatus* generally consisted of three types of behavior: immobilizing to escape detection, moving out of sight, and seeking permanent shelter. When caught, tail autotomy and vigorous struggling were utilized in an attempt to break free.

H. frenatus is not particularly cryptic with respect to the substrates on which it occurs. The lizard's ability to avoid detection is based on the area of the habitat it frequented (near the ceiling) and the poor light conditions.

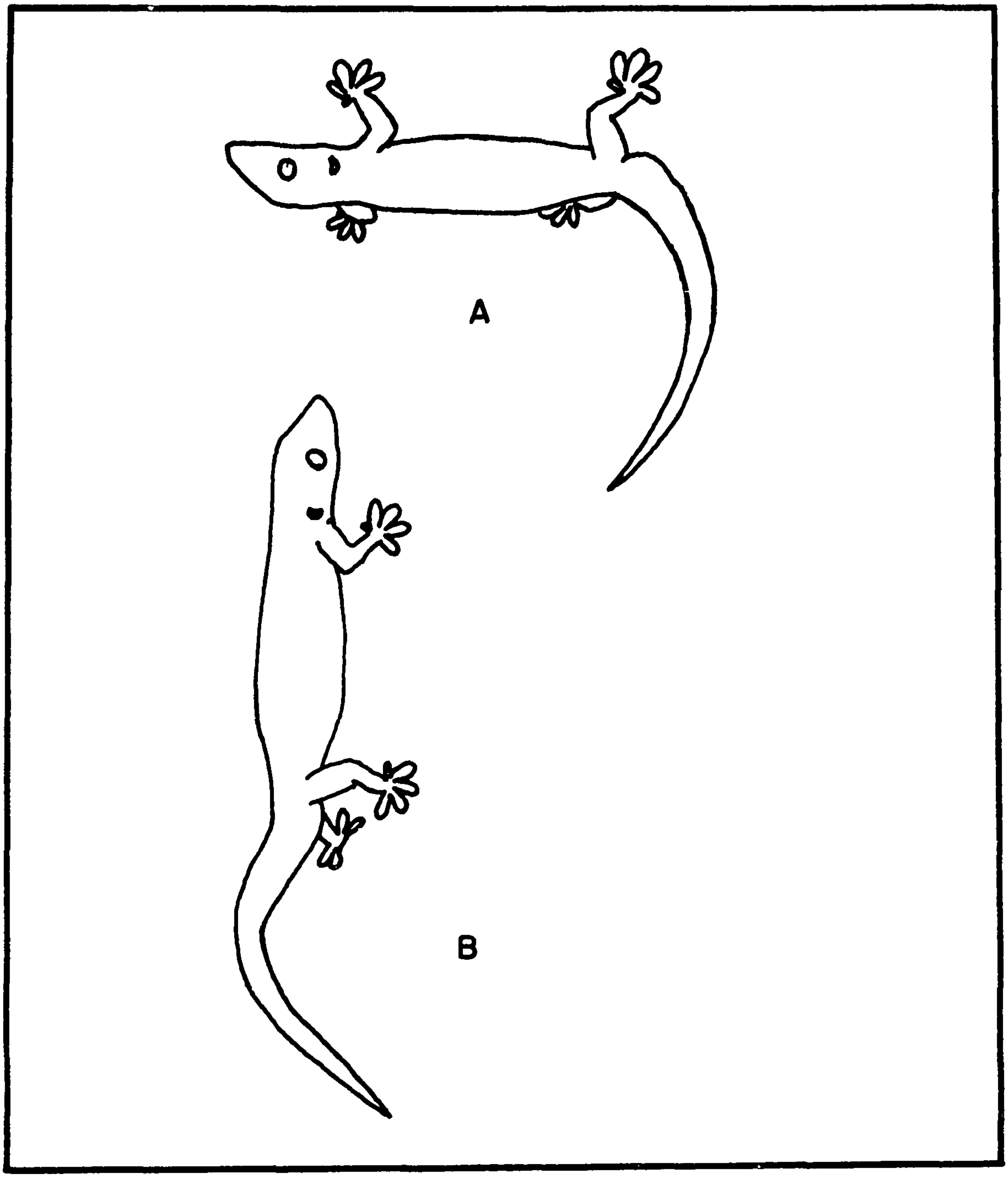


Fig. 13. Eliminative postures of *Hemidactylus frenatus* on ceiling (A) and on wall (B).

The lizard's habit of occupying the junction between surfaces also makes detection difficult.

Geckos frequently froze if approached, flattening against the substrate. Under such conditions lizards would often allow the observer to approach as near as a meter or less. More frequently, the animal would slip quickly to the opposite side of a ceiling beam or some such obstruction and remain out of sight.

If harassed, the geckos seek shelter which was generally close by. Places of shelter consisted of holes or cracks in the substrate. These refuges were generally high on walls and ceilings near the areas frequented by the geckos. In the absence of suitable high refuges, animals utilized cracks nearer floor level. Some geckos on the Doña María used the openings under room air-conditioners for retreats, and would move rapidly and directly down the wall to these places when pursued.

A few animals, on the walls and ceiling in the corners of the lower porch of the Doña María, utilized large bushy potted plants for retreats. If one of these lizards was vigorously pursued, it would leap from the wall into the potted plant where it was impossible to find. This did not appear to be merely an accident, since it occurred nearly every time the animals were harassed. It is not difficult to see that this type of behavior could have been derived from successful escapes due to slips.

Animals which lost their grip and fell, or were swept to the floor in the process of capture, nearly always landed dorsal side up. This cat-like ability was tested in captive animals. Geckos dropped from a height of five feet always landed dorsal side up, even if they were held ventral side up when dropped. This ability, no doubt, protects the geckos from injury and facilitates rapid escape after a fall.

After striking the floor a fallen gecko would, after a short hesitation, dash quickly into a darkened area. The animals appeared to seek regions with dim light conditions. If the lizard was not quickly found it would begin to ascend any convenient wall. The geckos were not content to remain dorsal side up on a horizontal surface.

After capture the gecko would usually wriggle vigorously, often shedding its tail during its struggles. Biting was also used to assist escape, but it was very infrequent and of doubtful value against any conceivable predator.

Animal associates

Although many types of animals occurred on the grounds of the Hotel Valles, only those that might have affected the geckos will be discussed.

Two invertebrates were conspicuous co-inhabitants of the gecko's habitat. Oriental cockroaches were numerous on all the structures of the hotel grounds. These insects, in the early instars, were used as food by the geckos. An unidentified species of large (10 cm leg span), aboreal, hunting spider was also very common on the hotel buildings. This spider fed on the roaches, and on one occasion an attack on a hatchling gecko was observed. The spider rushed out of a crack in the rock wall and attempted to grasp the hatchling. The lizard lost its grip and fell to the floor, thereby escaping the spider. This observation, and the habitat and habits of this spider, implicate it as a species predatory on _H._ _frenatus_.

The only reptile other than _H._ _frenatus_ seen in the Hotel Valles study area was _Sceloporus_ _variabilis_. A large number of these lizards lived on the outer stone walls of the buildings. Although their habitats were somewhat similar, no interactions between the nocturnal geckos and the diurnal _Sceloporus_ were observed. _Sceloporus_ are highly insectivorus and are, no doubt, limited food competitors of the geckos. It is also possible that the two species feed on each other's young. However, such relationships are probably infrequent due to species differences in 24 hour periodicity.

A large number of bird species occurred on the hotel grounds, but because of their diurnal habits, most had little effect on the geckos. An exception was the boat-tailed grackle, which was a possible predator of the geckos. Grackles were numerous on the grounds and would occasionally forage close to the buildings. On a number of evenings, grackles were observed on the Main Building porch feeding on insects trapped in porch lights. Geckos which frequented these areas at this time could also have been taken by these birds.

Potential mammalian predators consisted of domestic cats and opossums. The cats were the most obvious and successful predators of the gecko population. On nearly every night cats could be observed on and around the hotel buildings. On many occasions cats were seen apparently actively searching for lizards. These animals would gaze intently at walls and ceilings, stopping for a moment when they saw geckos. No actual capture of a gecko by a cat was observed, but on two occasions a cat was surprised while feeding on a gecko. On another occasion, a mutilated gecko carcass was found on the porch. The cats probably take geckos that happen to fall or stray too low on the walls. Opossums were not observed to feed on geckos, but being nocturnal, and common, they are also possible predators.

Social behavior

The social behavior of *H. frenatus* has been divided into three categories: courtship and copulation, aggression, and tail wag. The following data were obtained by observation and are largely descriptive.

Courtship and copulation.--Nine complete and 30 incomplete courtship-copulation encounters were recorded during the three month study. The following description is based on these observations and generalizes the variation noted. The successful mating sequence has been divided into five stages on the basis of male behavior: approach, initial hold, neck hold, copulation, and post copulation.

Approach.--Males occasionally called before approaching females, and this acoustic behavior will be discussed in Chapter V. Some males also performed a tail wag as they approached the female, but this behavior was rarely seen. More often males showed no apparent courtship behavior but merely rushed the female and attempted to secure a hold. Frequently stationary males were closely approached by females and their proximity seemed to stimulate the males to make an approach. The approach was a nonstop rush or lunge directly at the female with no special associated posture (Fig. 14A). The approach was over quickly, usually lasting only a fraction of a second.

Initial hold.--The rush of the male generally culminated with a jaw hold on the loose skin of the posterior part of the female's body (Fig. 14B), but occasionally a neck hold was directly secured. After the initial hold was made the female struggled violently, thrashing her body back and forth until she jerked free; or she quivered violently for a second or two before quieting. The initial hold was sometimes made on one of the legs of the female and, in all cases of this sort, the female escaped. If the female moved after quieting, she did so in a manner which brought her head toward the male's tail (Fig. 14B). The duration of the initial hold in nine matings varied from 30 seconds to two minutes, with a mean length of one minute 30 seconds.

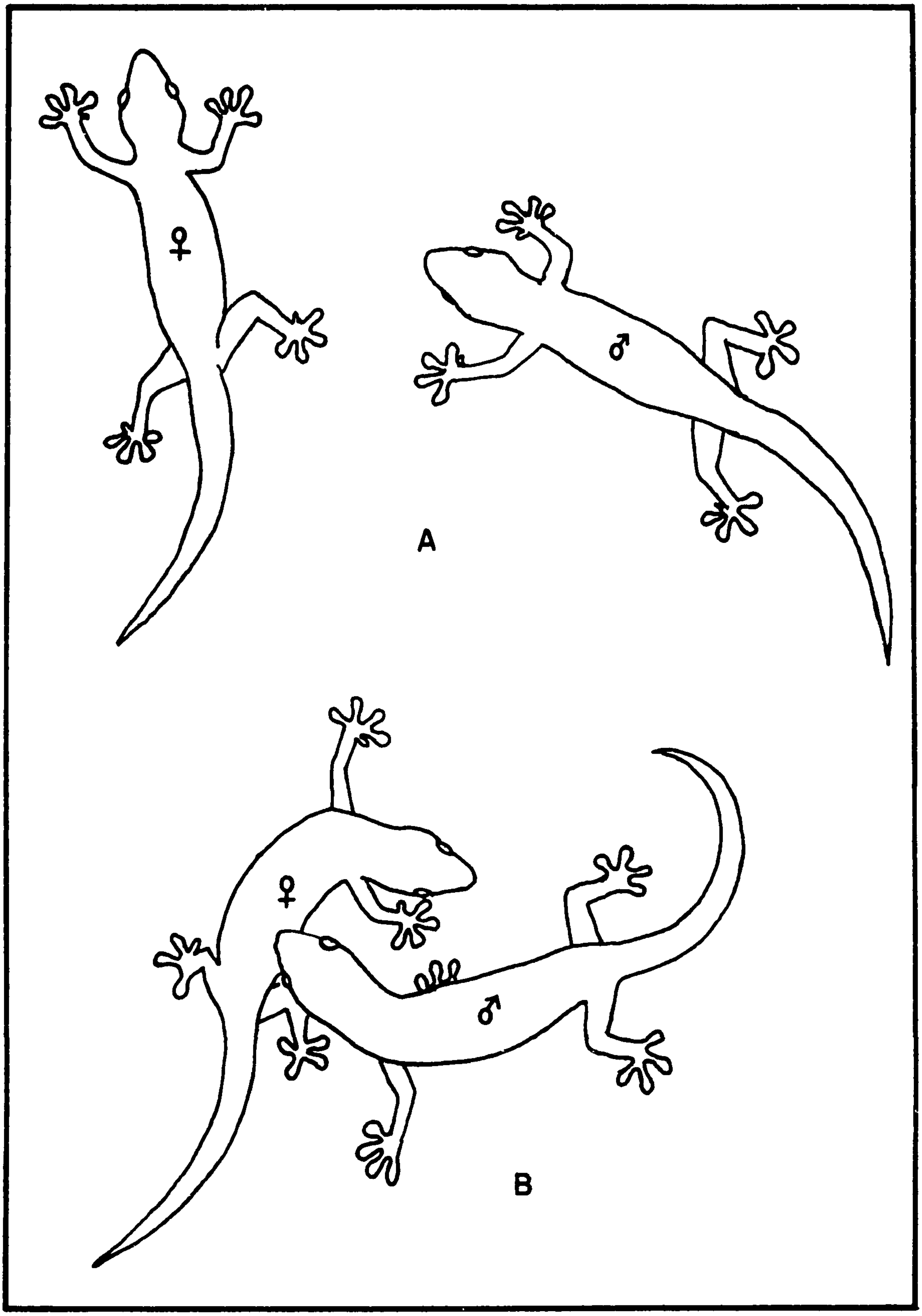
Neck hold.--If and when the female became quiet, the male shifted his hold forward toward the neck, often biting at flank or shoulder on the way. After obtaining a neck hold (Fig. 14C) the male brought his body parallel to the female's, and sometimes crawled forward a few steps dragging the female. Table 19 summarizes data on the initial and final positions of the male's grip on the female, showing the preponderance of the neck hold at copulation. The duration of this stage for nine matings averaged approximately one minute.

Table 19. Position of male's grip on female at initial hold and at copulation for nine completed matings of *Hemidactylus frenatus*.

	Flank	Shoulder	Neck
Initial	7	1	1
Final	0	1	8

Copulation.--The male swung his hindleg nearest the female across her pelvic region, and slipped his tail under that of the female, opposing his vent to hers (Fig. 14D). A hemipenis was inserted and insemination effected. Coitus duration for nine matings ranged from 5 to 20 minutes with a mean of 12 minutes.

Fig. 14. Stages of mating (A-E) and aggressive posture of male (F) of *Hemidactylus frenatus*.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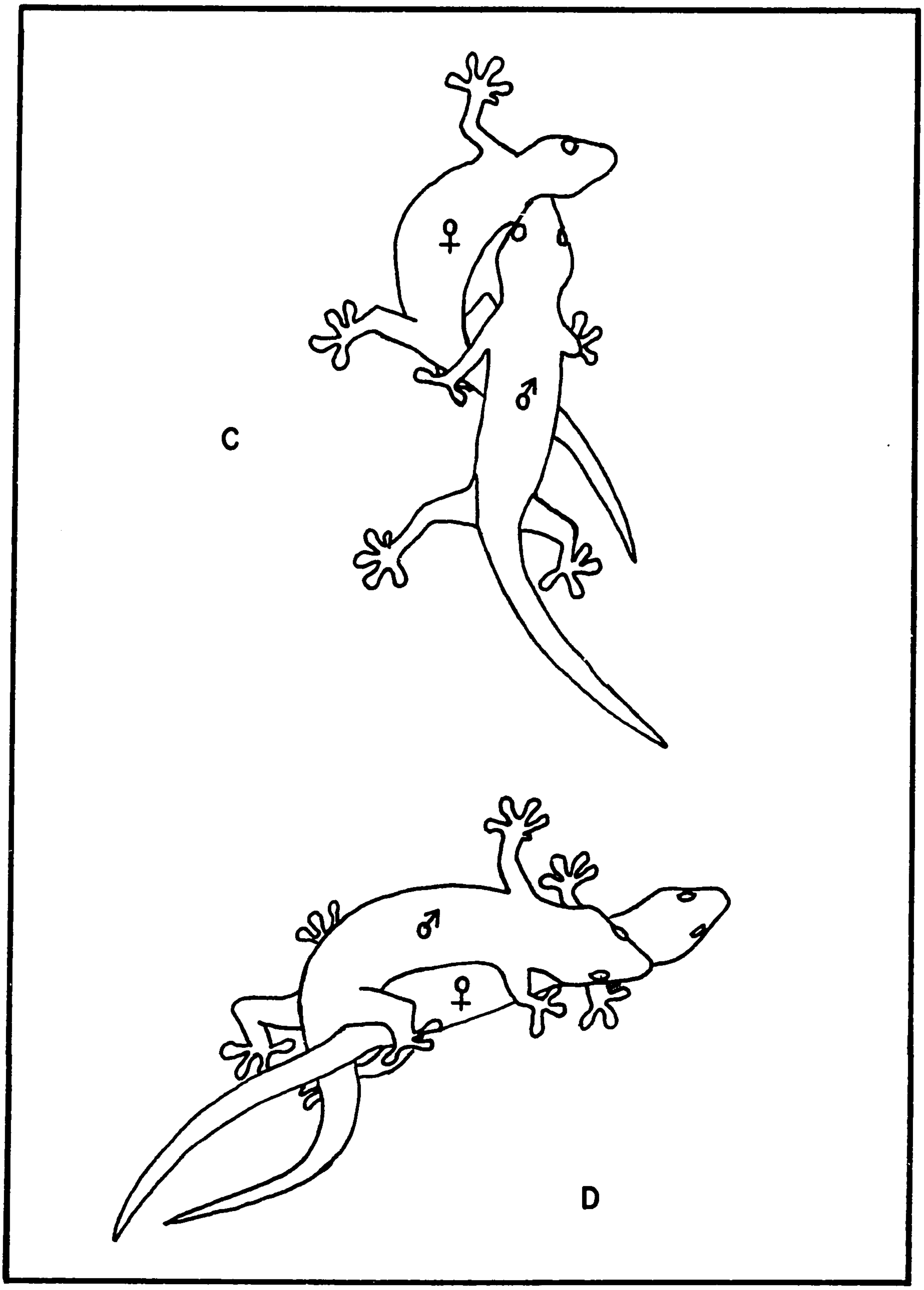
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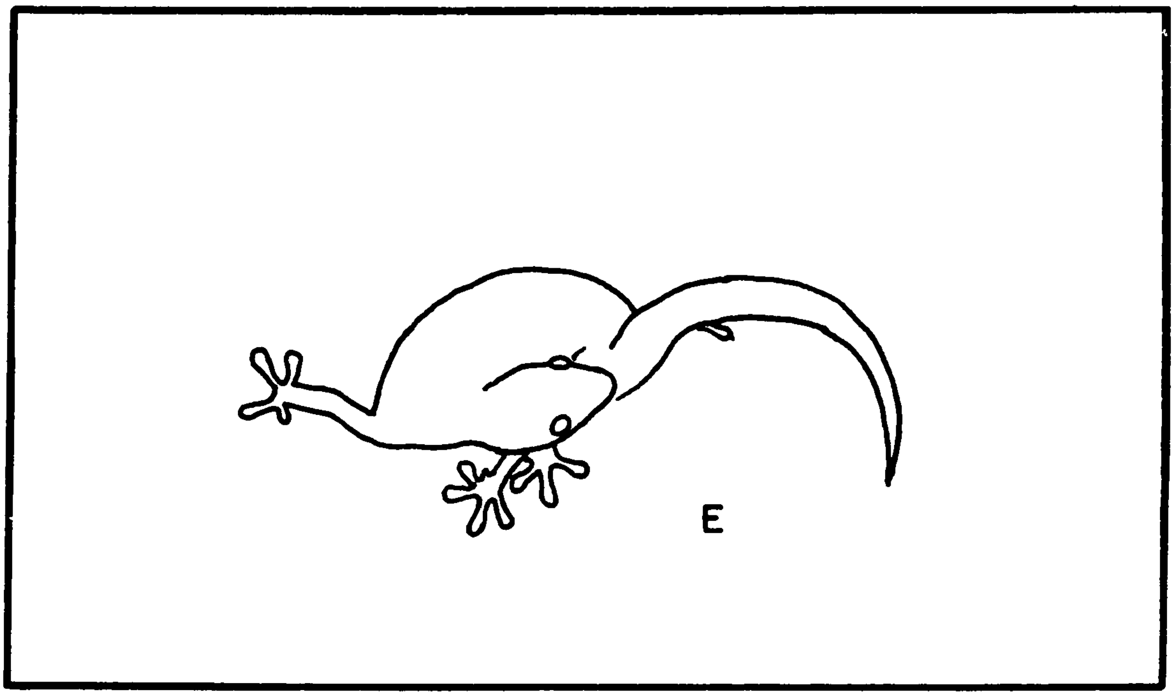
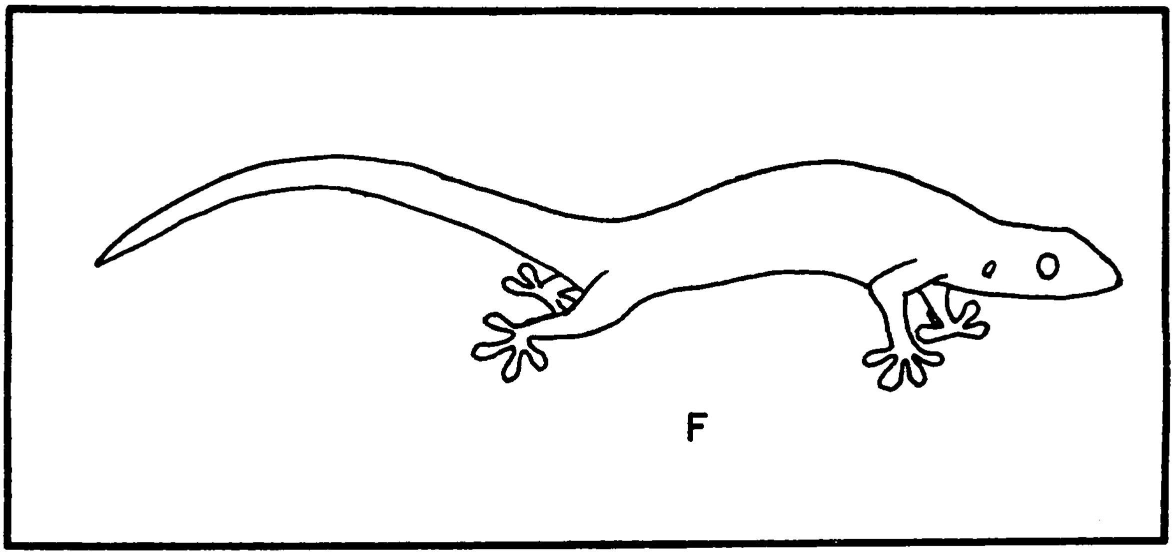


E



F

Post copulation.--Uncoupling was rapid; the male moved slightly backward off the female. The female often initiated uncoupling by struggling or moving. The male's back and tail were arched and the hemipenis still everted, after a moment the hemipenis was retracted and the back lowered. After uncoupling both sexes often turn and lick their cloacal regions for as long as a minute (Fig. 14E). Males also occasionally called after copulation.

Mechanisms of sex recognition in these geckos are not known, but it appears to be a matter of female response. If a female is unwilling to mate she repulses her suitor by force. Often she will reach back and bite the male, and the animals will whirl around before the male lets go. If a male attempted to mate with a young male member of his group, a vigorous struggle ensued. Males would not quiet down, and these homosexual encounters always ended at the initial hold stage.

Courtship and copulation in non-gekkonid species of lizards is generally quite similar to that in *H. frenatus*. A striking difference between the courtship of *H. frenatus* and that of many other species is found in the dependence in the former upon direct contact. Many lizards perform displays from a distance prior to mating (Carpenter, 1967). Involved in these displays are sexually dimorphic colors and movements. Male iguanids perform rapid shuddering movements of the head (courtship nods, Carpenter, 1967).

Diurnal geckos also utilize courtship displays prior to mating (Greer, 1967; Kastle, 1964). In the nocturnal *H. frenatus* and *Colenonyx variegatus* (Greenberg, 1943) contact seems to be the first essential element in mating. In the diurnal forms, the male's courtship behavior gives the female ample opportunity to escape, and anoestrous females are able to evade the male. In *H. frenatus* and probably other nocturnal geckos, the non-receptive female must reject the male by force after contact.

Acoustic behavior may play a role in sexual behavior and is discussed in Chapters V and VI.

Tail wag.--The tail wag is a slow sinuous movement of the tail used in asocial as well as social contexts. Young and adults of both sexes were observed performing tail wags while prey was stalked. All classes of geckos often utilized this behavior when they encountered another individual. Subordinate animals or social equals performed the tail wag more often than dominant animals. Dominant males only utilized this behavior upon meeting another large male, or prior to mating. Many times animals of both sexes were observed using the tail wag as they approached a large male. In all cases the tail wag appeared to occur at moments of high nervous tension.

The response to a tail wag was varied and appeared to depend upon the context in which it was given. The varied responses hinder any definite elucidation of the function of the tail wag. However, it appears that the wag may indicate submission, aggression and courtship.

The tail wag has been described for many lizards but in no case has a quantitative study been done to determine its significance.

Aggression.--Levels of aggression in H. frenatus varied with age and sex. Old males were the most aggressive, followed by young males. Females were never observed to exhibit aggressive behavior. Adult males were aggressive throughout their home ranges, although intensity of aggression was greater in certain areas.

H. frenatus were gregarious, living in small groups composed of one or occasionally two adult males, two or three adult females, and varying numbers of juveniles of both sexes. Dominance hierarchies were not studied but in each group one male appeared to be dominant over all other animals in the group. In limited laboratory observations the same type of despotism was noted.

Numerous aggressive encounters were recorded in the field, and these have been divided into two types. The first type was of low intensity and made up nearly all of the aggressive behavior noted. The low intensity encounters generally involved a young male and an adult male. The young animal would approach a foraging or stationary male and the adult would make a quick rush, chasing the younger off. The stimulus for attack is not known, and young males were apparently attacked or not attacked indiscriminately. Some animals were allowed to pass close to the male without any aggressive response, while others were attacked. No specific posture or display was associated with the low intensity encounters and they were completed within a few seconds. The attack was very similar to the mating approach and occasionally resulted in a jaw hold by the aggressor. The younger animal invariably escaped by wild thrashing. Occasionally (9 times) the attacked animal produced a single chirp vocalization on being bitten. Some adult males were observed to engage in these short aggressive forays eight or 10 times in an hour.

The second type of aggressive encounter was infrequently observed and of high intensity. Only 10 of these interactions were recorded, and all involved a pair of adult males. The first indication that such an encounter was imminent was the occurrence of an acoustic display by the resident male. In seven of the 10 encounters this call was answered by the non-resident. The resident then rushed toward the intruder, posturing as he came within a half meter. The intruder either turned tail and retreated (3 times) or postured in return (7 times). In the aggressive posture the head was held low and the back and tail were strongly arched with the legs partly extended (Fig. 14F). The posture appears to enhance the size of the individual. Posturing males positioned their bodies parallel to one another during the interaction, and oriented head-to-head, as well as in the head-to-tail "face-off", described for iguanid lizards (Carpenter, 1967). While posturing the animals strutted swiftly around one another. After only a few seconds one of the antagonists (usually the resident) gave another quite different call, and immediately attacked. The resident attempted to bite, but usually the other animal escaped and was chased for a few meters. On one occasion the resident grasped the other animal by the foreleg. The bitten animal struggled violently, broke free, and fell to the floor. At the conclusion of a high intensity encounter the victorious male may perform an acoustic display similar to the one given at the beginning of the encounter (9 of 10 interactions). High intensity encounters were generally short, lasting less than a minute from first call to last call.

Injuries as a result of aggression were common but superficial. Scars were evident on males' sides from wounds inflicted by biting. Also many broken tails probably resulted from aggressive interactions. Serious injury as a direct result of fighting was probably rare, but animals knocked to the floor during encounters were, no doubt, subject to greater predation pressure.

Aggressive behavior in non-gekkonids has been extensively studied. The early work by Nobel and Bradley (1933) has been followed by numerous field (Harris, 1964; Rand,

1967) and laboratory (Carpenter, 1963; Clark, 1965; Hardy, 1962) studies. Much of this work has been descriptive and has concentrated on the display behavior of these lizards.

Aggressive behavior in gekkonids has been poorly studied and consists largely of comments (Beebe, 1944; Church, 1962; Evans, 1936). A few excellent studies have been done, but these have dealt with aggressive behavior in diurnal geckos. Greer (1967) describes the aggressive behavior of two African species of Lygodactylus and Kastle (1964) describes the behavior of one species of Lygodactylus and three species of Phelsuma. No work has been found on aggressive behavior of nocturnal geckos, except for the work of Greenberg (1943) dealing with terrestrial Coleonyx.

In all lizard families studied aggressive behavior appears to be very similar. The behavior is composed of three parts which may vary in their order and importance; display, posture, and fight. The displays in diurnal lizards may consist of colors, or movements, or both. Associated with these displays are postures which may intensify the effect of the display. The above is true for diurnal geckos as well as for other families of diurnal lizards.

H. frenatus, and undoubtably other nocturnal geckos, possess the same facets of aggressive behavior as diurnal lizards, except that the display may be auditory rather than visual. The low light intensity precludes the use of color for display purposes, although presumably posture can be discerned. A description of the calls of H. frenatus is found in Chapter V.

Nocturnal geckos differ from most diurnal lizards in their apparent lack of female aggression (present study and Greenberg, 1943). In non-gekkonids female aggression has been reported in a number of studies (Carpenter, 1964; Harris, 1964; Tinkle, 1967). In diurnal gekkonids female aggression is also found (Greer, 1967; Kastle, 1964). The lack of aggression exhibited by female H. frenatus may be associated with the lack of courtship in these animals. The male does not lower the female's resistance by courtship activities but merely forces his favors on the female. Dominance of male over female is essential to mating in these lizards, and female aggression would be an interfering factor.

CHAPTER V

ACOUSTIC BEHAVIOR

Introduction

Bio-Acoustics is a scientific discipline which has made enormous strides during the past decade. Work has been done on a wide variety of animal types with a preponderance being in arthropods and vertebrates. Within the vertebrates the majority of the investigations have dealt with four groups; fish, amphibians, birds, and mammals. The acoustic behavior of reptiles, however, has received little study.

Sound producing mechanisms are absent in most reptile species, but occur in at least some members of the four surviving Orders. Vocalization has been reported in association with reproductive activities of various turtles, but its significance is not known (Auffenberg, 1965; DeSola, 1930; Evans, 1961; Pope, 1946). Vocalization in the Crocodilia is common and is thought to be involved with territoriality and courtship (Evans, 1961; McIlhenny, 1935). Snakes produce sounds by rattling, stridulating and glottal hissing that are thought to be largely warning signals (Blair, 1968). Sound production is lacking, or is limited to hissing in most groups of lizards, but a few can produce distinct vocalizations. The family Gekkonidae is noted for its vocal abilities. A few other lizards such as the leopard lizard (Crotaphytus wislizenii) do have distinct calls (Wever et al., 1966). Except for the geckos, and possibly the few rare examples such as the leopard lizard, vocalization seems to be of little significance in communication among lizards.

The significance of gecko sounds has been a source of controversy and speculation for years. Many early field observations are suggestive, but most statements remain unsupported by conclusive evidence. Functional suggestions for the call range from attraction of insects (Beebe, 1944) to the more plausible suggestion that the call functions 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 no functional classification of the calls of a gecko species has been published.

Reviews of investigations with anuran amphibians (Blair, 1968), birds (Marler, 1960), and mammals (Tembrock, 1963) have shown that most species produce vocalizations which serve species-specific functions. The recent work with visual displays of iguanid and agamid lizards (Carpenter, 1967; Ferguson, 1969; Jenssen, 1969) demonstrates the importance of this behavior in the social activities of the species, and indicates that such behavior may be a useful tool in taxonomic studies.

The auditory sensitivity of gecko ears has been studied by Wever and his co-workers at Princeton (see Chapt. VI for discussion). However, the acoustic behavior of geckos remains virtually unknown, in spite of the common knowledge of its existence, and the strong precedents for acoustic study from other vertebrates.

In the present work the description and analysis of the vocalizations and acoustic behavior of _H_. _frenatus_ are presented and discussed. The possible species-specific nature of the calls is also suggested.

Methods and Materials

Observations were made on marked animals of both sexes, and the types of calls noted as well as the contexts within which they were given. Gecko calls were counted for an hour at sundown on nearly every other night, and on five nights hourly call counts were made from sundown to sunrise.

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 and flutter ± 0.15% r.m.s. @ 3 3/4 i.p.s. A Sennheiser cardioid microphone with built-in windscreen and frequency response of 70 to 14,000 Hz was used in conjunction with a 24 inch diameter parabolic reflector. Graphic analysis of the calls was accomplished with a Kay model 7029A sonagraph.

It has been pointed out (Watkins, 1967) that the sonagraph is not infallible, and that frequency interpretations derived from sonagrams are subject to error. The frequency interpretations in this paper should be considered tentative until corroborated by other means of analysis.

The method of recording was dictated by the habits of the geckos. Early in the study it was discovered that recordings of the calls of visible animals would be difficult to obtain. Animals in well lighted areas, applicable to observation, rarely called and if they did call, it was from a secluded location. Also the frequency of calls from any one individual was low and unpredictable. In order to obtain sufficient calls for description and analysis, it was necessary to record unidentified and unseen geckos. Three separate recording sites were used, two on the Main Building and one on the Doña María. The parabolic reflector was pointed in a different direction at each recording site in an attempt to increase the number of individuals recorded. The recording sites were rotated and recordings made on nearly every other night. The time of recording varied and nearly all hours of the night were included, but most recordings were made during the two hours following sunset.

A few recordings were made of identified free-living geckos and of captive animals. Captive *H. frenatus* were kept in small (30/30/90 cm) wire mesh cages and were recorded without the use of a parabolic reflector.

Work involving species other than *H. frenatus* was done with captive animals at the Animal Behavior Laboratory of the University of Oklahoma. The methods of recording and analysis were the same as those described for *H. frenatus*.

All bio-acoustic terminology utilized in this work follows that suggested by Broughton (1963).

Results and Discussion

Contextual observations and recordings of vocalizations demonstrated at least three functionally and physically distinct types of calls. These will be considered, more or less, in their order of importance.

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 three month study period. This call was given by adults of both sexes, but much more frequently by males. Dominant males of a group were especially vocal, and most of the data and discussion are derived from MC calls of these animals. Geckos of less than 45 mm in snout-vent length were not observed to utter the MC call; it is possible, however, that they have the ability to do so.

Although these calls were quite numerous it was extremely difficult to observe an animal in the process of calling. The geckos often called from a secluded spot, and this, plus the short duration of the call, and the lack of associated vigorous body movements, made calling individuals difficult to locate. The 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.

Context.--The contexts within which the MC call was given were varied. The call may be uttered with no apparent stimulus by solitary animals 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.

The calls that appeared to have no associated stimulus might have been the result of an allelomimetic effect. It was observed that captive geckos could occasionally be stimulated to call by the playing of a recorded call near their cage. Free-living geckos also appeared to answer the calls of other geckos, but this was impossible to verify, except in specific situations, due to the large numbers of calling animals.

The MC call was also commonly given at the conclusion of various activities. On three occasions a very low intensity call was heard after eliminative behavior. The call was occasionally performed after successful feeding (15 times) and after many matings (17 observations). Nine of the 10 high intensity aggressive encounters were concluded with a MC call by the victorious male.

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 if the distance between the geckos was small. The gecko at which the call was directed occasionally answered with a MC call (6 times). Calling between aggressive males was observed 25 times and was followed by high intensity aggressive encounters 10 times. Males were not observed to direct a MC call to another male in their group. In 8 of 30 courtship-copulation encounters observed males uttered the MC call prior to approaching the female. On no occasion did a male direct a MC call to a juvenile.

Females were observed to use the MC call with no apparent stimulus three times, and by one female when approached by another female. A captive female gave the MC call in response to a recorded male call on three occasions, but numerous other females failed to respond to the same call.

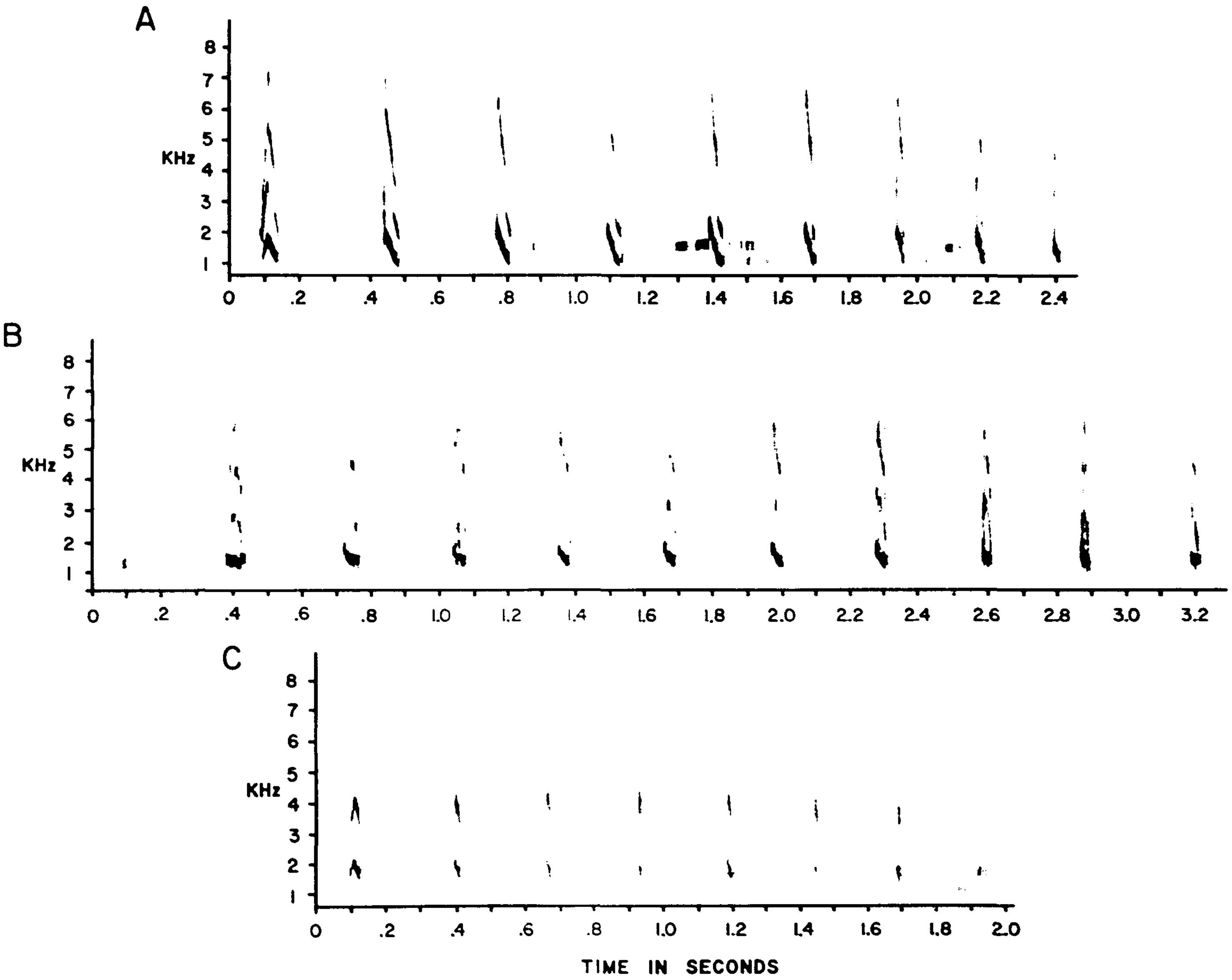
The variable contexts within which the MC call is given make functional interpretations difficult. For the most part the call occurs when the animal is in an excited state, especially in social situations. The extensive use of the call by males in apparent territorial disputes ties the MC call rather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

Much more work must be done to elucidate the vocal repertory of other species of geckos before accurate call comparisons can be drawn between species. However, it appears that most of the calls mentioned in the literature are similar in context to the MC call of *H. frenatus* (Beebe, 1944; Brain, 1962; Evans, 1936; Loveridge, 1947; Mertens, 1955; Petzold, 1965; Schmidt and Inger, 1957), and are also probably involved in agonistic behavior and territoriality.

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 a very low intensity and could barely be heard two meters away. Other MC calls were always easily audible from nearly 150 m distant. Calls directed at other males were always the loudest, being audible from over 150 m away.

The MC call of *H. frenatus* is composed of a series of chirps; "gack-gack-gack"; suggestive of the barking of a very small dog. Figure 15 shows sonagrams of MC calls from three different adult male geckos. Figure 15B is a sonagram of a recording made of a captive animal and is

Fig. 15. Sonagrams of the multiple chirp (MC) call of three adult male *Hemidactylus frenatus* recorded in Ciudad Valles, S.L.P., Mexico 1969.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TIME IN SECONDS

completely free of background noise. Figures 15A and C are sonagrams of the calls of free-living geckos and show attendant background noise between the chirps. The dominant frequency of each chirp ranges from 1500 to nearly 2500 Hz with harmonics at approximately 2000 Hz intervals above the dominant. Most of the sound energy is in the first two or three harmonics. In the first chirp of the calls the dominant frequency appears to rise from 1500 to 2000 Hz and then drop back to 1500 Hz. In the subsequent chirps the pitch descends from 2000 to 1500 Hz. The frequency range shown in Fig. 15 is from below 1000 to over 8000 Hz, and further sonagraphic analysis shows harmonics that reach frequencies of over 14,000 Hz. The three sonagrams shown in Fig. 15 are very similar in their physical aspects as were all the calls graphed.

Statistics of three parameters of the MC call are shown in Table 20. The number of chirps per call averaged approximately nine, with a range of 5 to 15. The number of chirps per call varied with each vocalization of an individual, and seemed to be related to intensity of stimulation for the call. The duration of the call averaged approximately two seconds and also probably varied with emotional state as well as with temperature. The mean call rate was 4.51 ± 0.68 chirps per second, and varied in response to temperature.

Table 20. Statistical evaluation of the number of chirps, duration, and rate of 143 *Hemidactylus frenatus* multiple chirp calls recorded at Ciudad Valles, S.L.P., Mexico, March-May 1969.

	Number of Chirps	Duration of Call in Seconds	Rate in Chirps per Second
Range	5 - 15	1.05 - 3.73	3.12 - 5.82
Mean	8.78	1.97	4.51
Standard Deviation	1.75	0.48	0.68

Effect of temperature on call.--Fig. 15 shows two calls (A and B) recorded at approximately the same temperature (25 C), and one (C) recorded at a higher 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. 16 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 inaccuracy it is obvious that call rates increase with an increase in temperature.

A regression analysis was performed on the data and a regression line drawn (Fig. 16). A highly significant ($P < .001$) positive correlation exists between calling rate and temperature as determined by an F test for regression. The call rate in this temperature range may be calculated

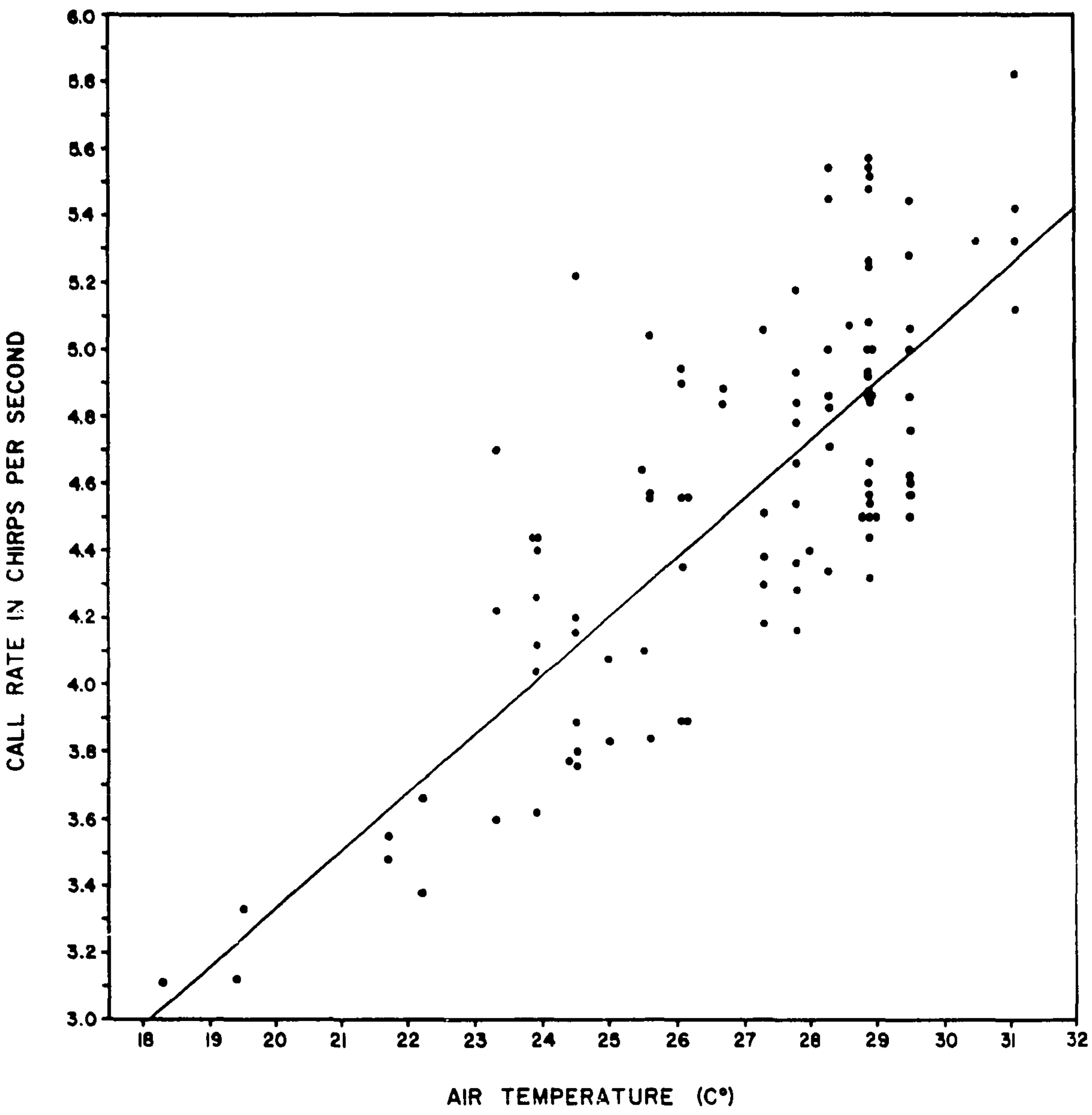


Fig. 16. Relationship of rate of multiple chirp call (expressed in chirps per second) and air temperature with calculated regression line for 143 _Hemidactylus frenatus_ calls recorded at Ciudad Valles, S.L.P., Mexico, March-May 1969.

through the use of the formula $y = 0.17x - 0.04$ where y is an estimate of the number of chirps per second and x the air temperature in centigrade degrees.

The fact that the rate of a call increases with higher temperatures is not surprising in light of the many studies on rates of biological processes 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 increase with increasing temperature. In anurans it has also been demonstrated that the dominant frequency increases slightly with temperature (Blair, 1958). The dominant frequency may also increase with temperature in gecko calls, but the data are insufficient for accurate analysis.

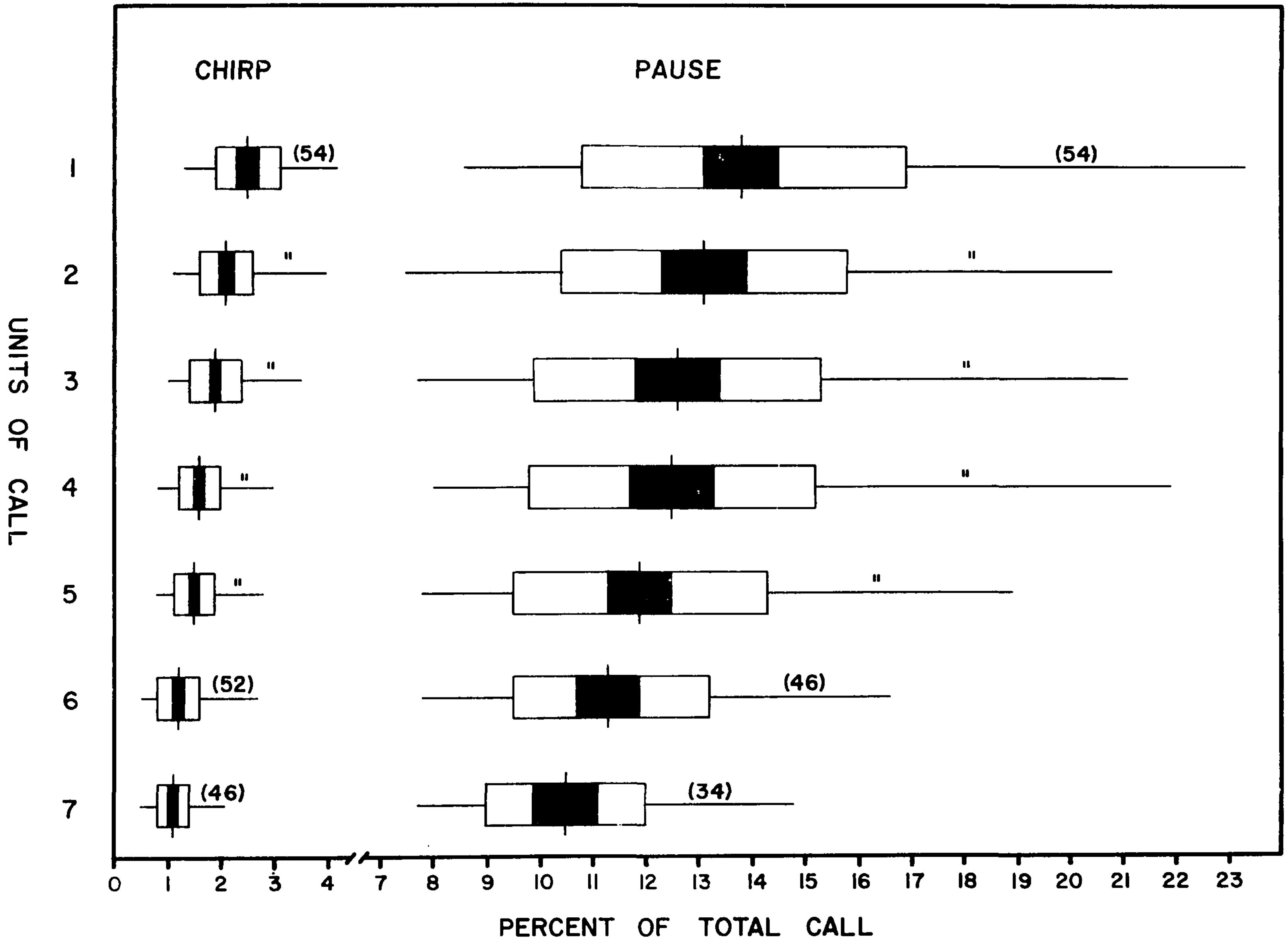
The effects of temperature on the auditory sensitivity of lizards has been studied by Campbell (1969). He found the greatest auditory sensitivity within the range of preferred body temperatures. The two geckos studied by Campbell (_Coleonyx variegatus_ and _Gecko gecko_) both have their highest auditory sensitivity at the upper end of their activity temperature range. The wide activity temperature range of _H. frenatus_ would seem to require auditory sensitivity over a wide range. More work is needed to determine the effects of temperature on gecko audition and vocalization.

Temporal pattern.--The 54 clearest sonagrams were chosen, and individual chirps and pauses were timed to the nearest 0.01 of a second and estimated to the nearest 0.001 of a second for seven chirp-pause units. Chirps varied in duration from a mean of 0.045 ± 0.009 seconds in the first unit to a mean of 0.022 ± 0.008 seconds in the seventh unit. A standard deviation of less than ± 0.05 for all seven chirps and pauses indicates a high degree of constancy.

The timings of chirps and pauses, and the sonagrams in Fig. 15, indicate that a temporal pattern exists in the MC call. The duration of each individual chirp and pause appears to shorten as the call progresses. To show this temporal pattern, and to determine if other patterns exist, 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 the temperature effects discussed previously.

Fig. 17 shows ranges, means, standard deviations and 95% confidence limits for each chirp and pause. The chirps and pauses obviously shorten with each additional unit. Using the 95% confidence limit overlap test it can be seen that a significant difference exists between the means of early and late parts of the call. The standard deviations indicate that both chirps and pauses become less variable as the call progresses, but this is probably a reflection

Fig. 17. Duration of chirps and pauses of the multiple chirp call of *Hemidactylus frenatus* (expressed as a percent of total call) from Ciudad Valles, S.L.P., Mexico, March-May 1969. Horizontal lines show observed ranges; rectangles mark standard deviation with solid black indicating 95% confidence intervals for the means. The means are indicated by vertical lines, and the number of records for each chirp and pause is shown in parenthesis.


CHIRP
PAUSE
UNITS OF CALL
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2
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5
6
7
(54)
(54)
(52)
(46)
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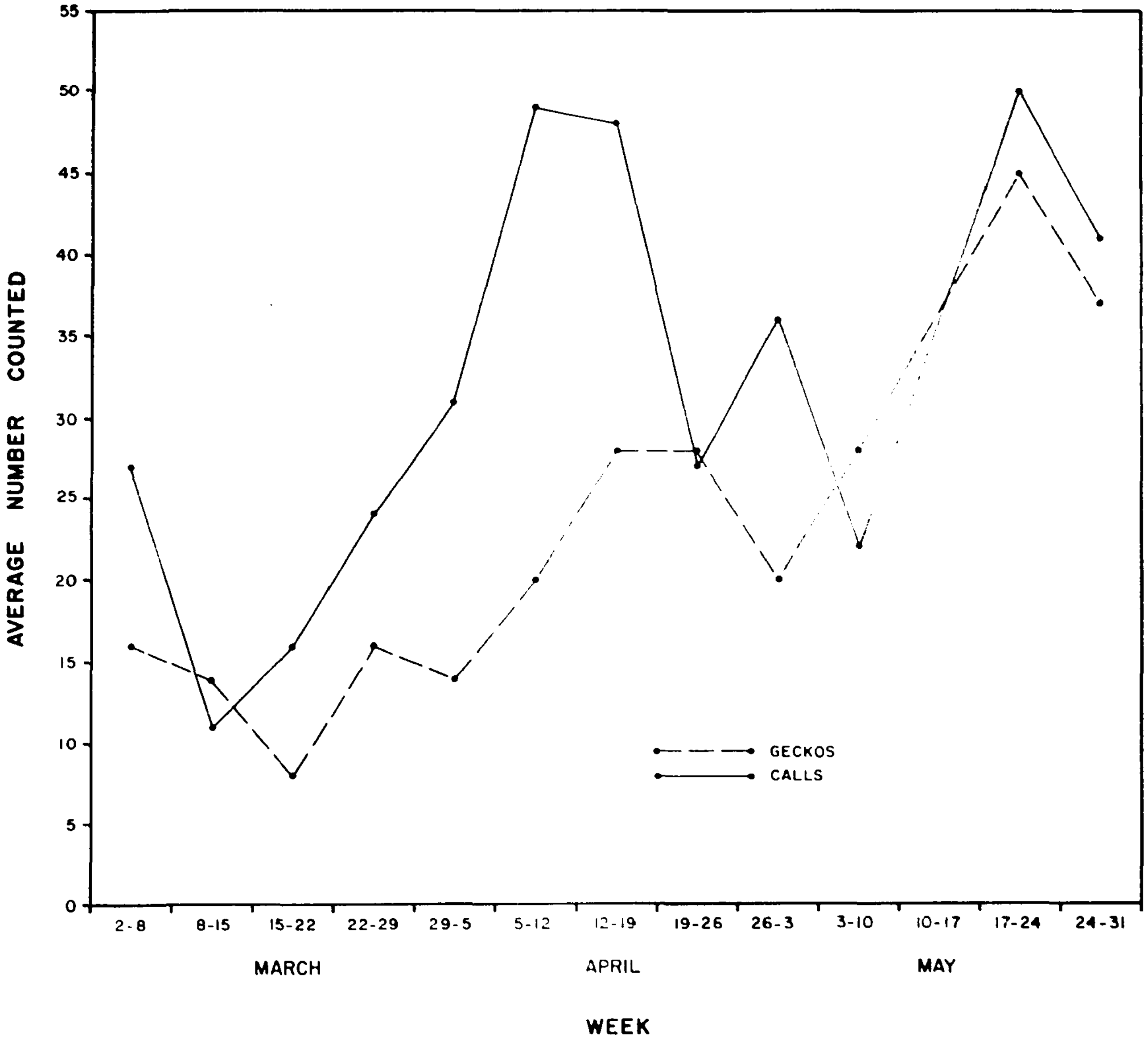
22
23
PERCENT OF TOTAL CALL

of the difficulty in accurate measurement of the shorter time intervals. The temporal pattern shown in Fig. 17 was noticeable in all graphed calls.

Calling periodicity.--The average daily number of MC calls counted for one hour at dusk was calculated for each week of the study. The call data are plotted with average weekly number of geckos at daily 10 PM census in Fig. 18. Average daily call counts per week increased over the study period from 27 in the first week of March to 42 in the last week of May. The highest weekly average was 49 in early April and the lowest was 11 in early March. The average number of geckos censused was closely correlated to the average number of calls counted, but the former is generally a lower number. This is expected since the gecko census was taken over a small area while all audible calls were counted.

In Chapter IV it was demonstrated that the average weekly number, of geckos censused per day, was closely correlated with environmental temperatures (Fig. 11). Since the average weekly number of calls is closely correlated with average number of geckos censused it is apparent that temperature determines call numbers by controlling activity. Early in the study temperatures were low, few geckos were out, and calls were correspondingly scarce. Later in the study temperatures rose, with a concurrent rise in active geckos and vocalizations. Disproportionately

Fig. 18. Mean weekly number of multiple chirp calls of *Hemidactylus frenatus* counted daily in one hour at dusk, compared to mean daily number of geckos censused per week. Ciudad Valles, S.L.P., Mexico, March-May 1969.


AVERAGE NUMBER COUNTED
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5
0
2-8
8-15
15-22
22-29
29-5
5-12
12-19
19-26
26-3
3-10
10-17
17-24
24-31
MARCH
APRIL
MAY
WEEK
GECKOS
CALLS

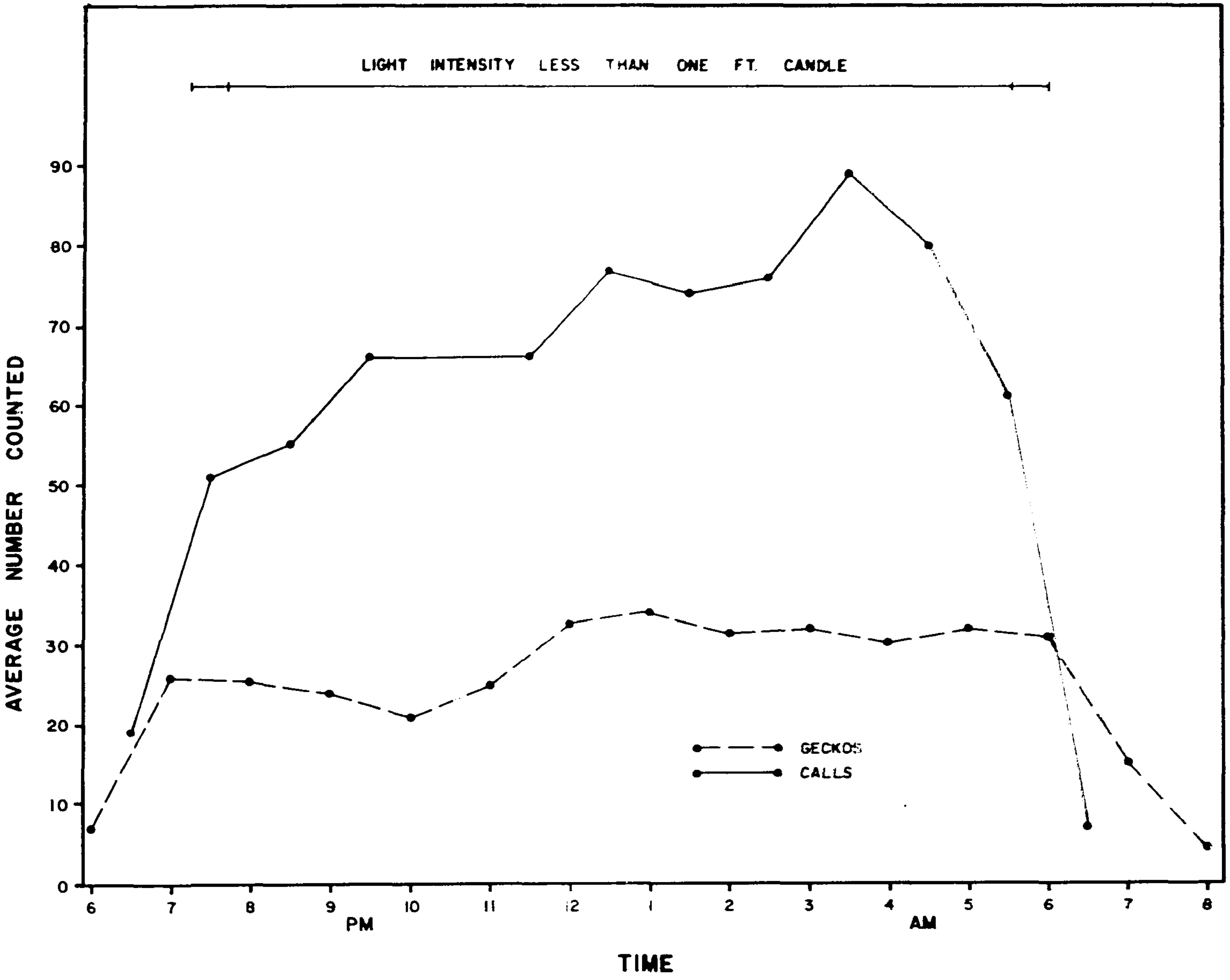
large differences between call numbers and geckos censused, such as those during early April, might be due to physiological factors, but this could not be determined in such a short term study.

Twenty-four hour calling periodicity was determined by hourly counts on five nights; March 28, April 8 and 21, and May 1 and 21. Average hourly call counts and gecko counts (porch census area) are plotted with hours of light intensity less than one foot candle in Fig. 19. Calls increased from an average of 19 per hour from 6:00 to 7:00 PM to a high of 89 per hour from 3:00 to 4:00 AM, and then dropped to a low of seven calls at dawn.

As in weekly periodicity the average number of calls per hour is correlated with the average number of geckos censused. Again 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 are censused. The limits of vocal activity are apparently determined by light intensity, with few calls occurring during daylight hours.

The average number of calls is closely correlated with the numbers of geckos censused, except for the period from 2:00 to 5:00 AM 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 of

Fig. 19. Mean number of multiple chirp calls of *Hemidactylus frenatus* per hour, mean hourly gecko census, and hours of light intensity less than one foot candle for five nights. Ciudad Valles, S.L.P., Mexico, March-May 1969.


LIGHT INTENSITY LESS THAN ONE FT. CANDLE
AVERAGE NUMBER COUNTED
0
10
20
30
40
50
60
70
80
90
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
PM
AM
TIME
GECKOS
CALLS

night. 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.

Three authors have mentioned diel calling periodicity in nocturnal geckos. Brain (1962) states that *Ptenopus garruius* calls in the late afternoon, with a maximum at sundown and the calls die away as darkness falls. Loverage (1947), also working with *Ptenopus 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. None of these authors gives numerical data to substantiate these statements. The differences between these geckos and *H. frenatus* might be due to actual specific differences in calling periodicity, or merely to a lack of detailed study by these investigators.

Churr call

The churr call is an infrequently heard vocalization of *H. frenatus* that is closely associated with aggressive interactions. Twenty-three of these calls were heard during the three month study period, only 10 of which were produced by geckos under observation.

Context.--The context of the churr call was highly specific. All 10 churrs were uttered by adult males during high intensity 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 (under 45 mm snout-vent length) were observed to utilize this vocalization.

The churr in _H_. _frenatus_ is strictly a fighting call. It probably functions as a last moment warning or intimidation, and allows the attacked animal to begin his retreat before bodily harm is inflicted.

A call similar in context to the churr has been reported in Tokay geckos (Wever et al., 1963b) and in _Nephrurus_ _asper_ (Bustard, 1967b). These large geckos are belligerent and when disturbed by a human or another gecko they open the mouth 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 Tokays the call may be performed by both sexes, but much more frequently by males.

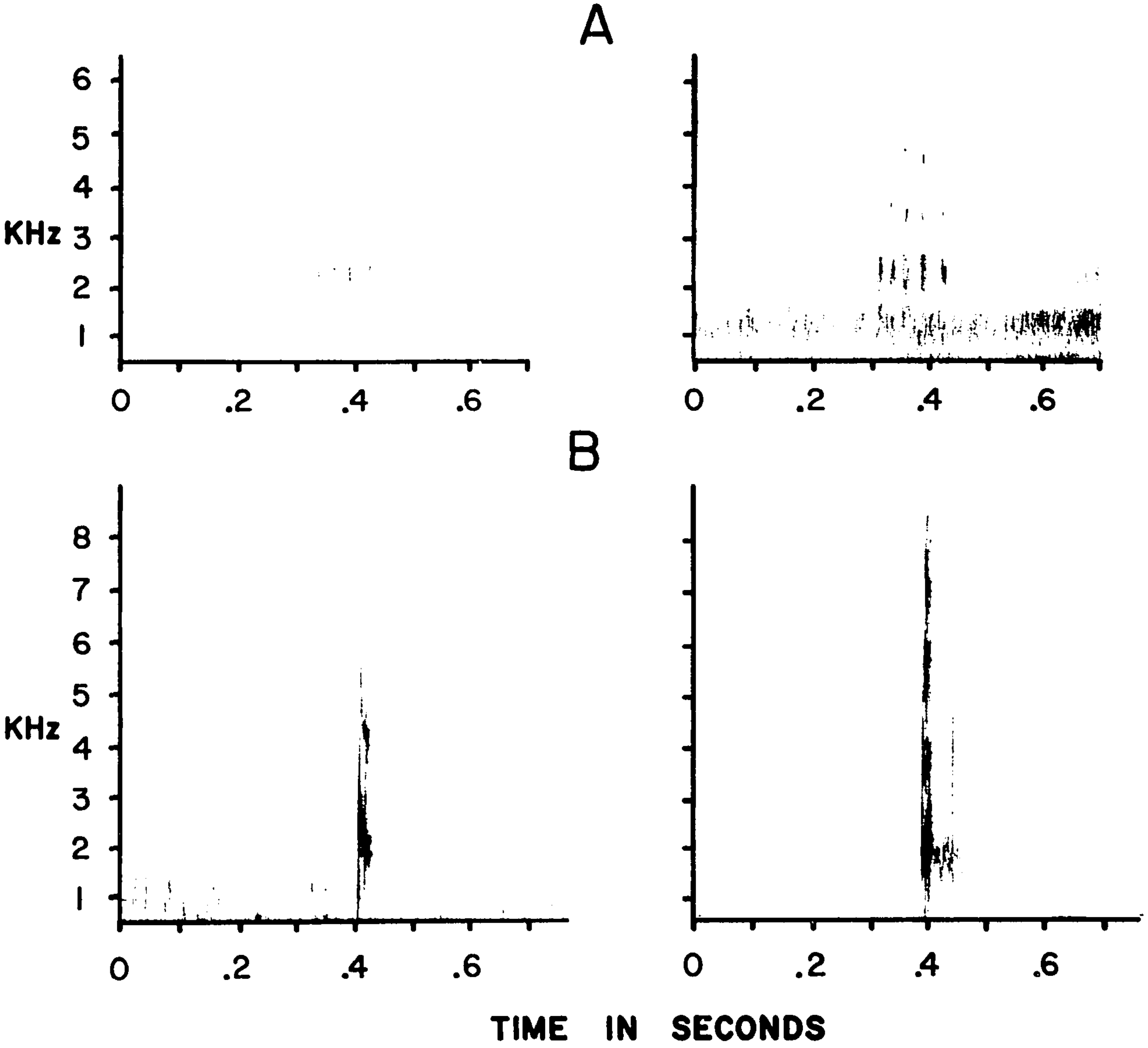
Description.--The churr is an extremely rapid series of short chirps similar in sound to the rattle of a high speed teletype machine. Figure 20A shows sonagrams of this call for two males. These sonagrams are of the only two churr calls recorded, and both suffer from low intensity and background noise 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 duration of the two recorded calls is less than 0.2 of a second, and the other churrs heard appeared to be of similar duration.

The loudness of the churrs was relatively consistent and they were audible from approximately 35 meters distant under good conditions.

Single chirp call

A frequently heard call that is involved with distress is the single chirp (SC) call. Hundreds of these calls were heard while handling animals, and from caged captive animals. 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 under 35 mm in snout-vent length was observed to utter the SC call.

Fig. 20. Sonagrams of churr calls (A) and single chirp calls (B) of *Hemidactylus frenatus* recorded at Ciudad Valles, S.L.P., Mexico 1969.


A
B
KHz
6
5
4
3
2
1
8
7
0
.2
.4
.6
TIME IN SECONDS

Context.--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. If a large number of geckos were placed in a small cage, a great deal of low intensity aggressive behavior ensued, and SC calls were produced. On nine occasions SC calls were observed to follow low intensity aggressive encounters between free-living males. As the aggressor bit his victim the bitten animal gave the SC call, struggled and invariably escaped.

The single chirp call is obviously closely associated with distress, but its function in aiding the gecko is not known. The production of the chirp expells air from the lungs making the lizard slightly smaller, and the sound produced, although of low intensity, might act to startle a predator or aggressor. These two aspects of the call may aid the lizard to escape.

The involvement of the SC call in low intensity aggressive encounters may also implicate it as a release call. The low intensity aggressive encounter, as was pointed out in Chapter IV, is very similar to mating beahvior. It is possible that the SC call signals a male that he has grasped another male.

Vocalizations as a result of handling are known to occur in Cnemidophorus (Wever et al., 1966) as well as in some geckos (J.R. Dixon, personal communication; Evans, 1936). In all cases these are short chirps or squeaks and their functional significance is not known.

Description.--The chirp is a single short pulse of sound; "gack"; similar to the individual pulses of the multiple chirp call. Two sonagrams of single chirps are shown in Fig. 20B. The dominant frequency of the chirp is approximately 2000 Hz, with harmonics at 1000 Hz intervals above the dominant. The duration of the chirp is very short (less than .05 of a second) and it begins and ends abruptly. The two chirps shown are of female (Fig. 20B left) and male (Fig. 20B right) calls in response to rough handling. Calls of captive males during aggressive interactions were also recorded, and they appear identical to the graphed single chirps.

The loudness of the SC call varies; some chirps can only be heard from a few meters away while others are clearly audible from 10 meters. The level of intensity does not seem to be correlated with context, and the reasons for these variations are not known. In general this call is of lower intensity than the others previously discussed.

Species-specific aspects of multiple chirp call

Recent investigations concerning species-specific stereotyped behavior in anuran amphibians, birds, and mammals has stimulated thinking concerning its taxonomic usefulness. Hinde and Tinbegen (1958) and Mayr (1958) have described stereotyped behavior in vertebrates and discussed its value to systematic zoology. Taxonomists are interested in studying genetic relationships between groups, and thus stereotyped behavior must be genetically controlled and variation within the group must be less than variation between groups. Some aspects of the acoustic behavior of insects (Dumortier, 1963), anurans (Bogert, 1960), birds (Marler, 1960), and mammals (Tembrock, 1968) have been found to meet these criteria, and have demonstrated taxonomic usefulness.

Species-specificity of gecko calls has not been studied, but Werner (1965), in his study of three subspecies of *Ptyodactylus* geckos in Israel, states that the males of two of the species call differently. No quantitative evidence is provided for this statement.

To determine possible species-specific differences in the MC calls of geckos, a superficial comparison will be made between the calls of *Hemidactylus frenatus*, *Hemidactylus turcicus*, and *Phyllodactylus magnus*.

Specimens of *H. turcicus* were collected on a motel in Tampico, Mexico on 29 March 1968, and observed in captivity during the summer of 1968. Multiple chirp calls were performed primarily by males in agonistic contexts. The frequency of calling was low and only portions of seven calls were recorded. The calls were long, averaging four seconds in duration with up to 17 chirps (average 13) in a call. No temporal pattern could be established. The intensity of the calls was low, being audible from approximately four meters away.

Specimens of Phyllodactylus magnus were collected on trees and fence posts west of Tehuantepec, Mexico on 24 March 1968. These animals were observed in captivity during the summer of 1968. Most of the multiple chirp calls were performed by males in agonistic encounters. Calling predictability and frequency was low and only portions of 10 calls were recorded. The calls consisted of an average of 7.5 chirps with a mean duration of 2.1 seconds. A temporal pattern could not be established. Calling intensity was very low and calls could only be heard from two or three meters away.

Sonagrams of portions of the calls of H. frenatus, H. turcicus, and P. magnus are compared in Fig. 21. The three calls chosen were recorded at an air temperature of approximately 27 C, minimizing differences due to temperature effects. Critical comparison is limited because of differences in level of background noise and call intensity. The sonagram for H. turcicus is further complicated because the calls of two individuals are superimposed, but only the stronger five chirp call will be considered.

Species differences in duration of pauses and chirps, intensity pattern of chirps, and physical characteristics

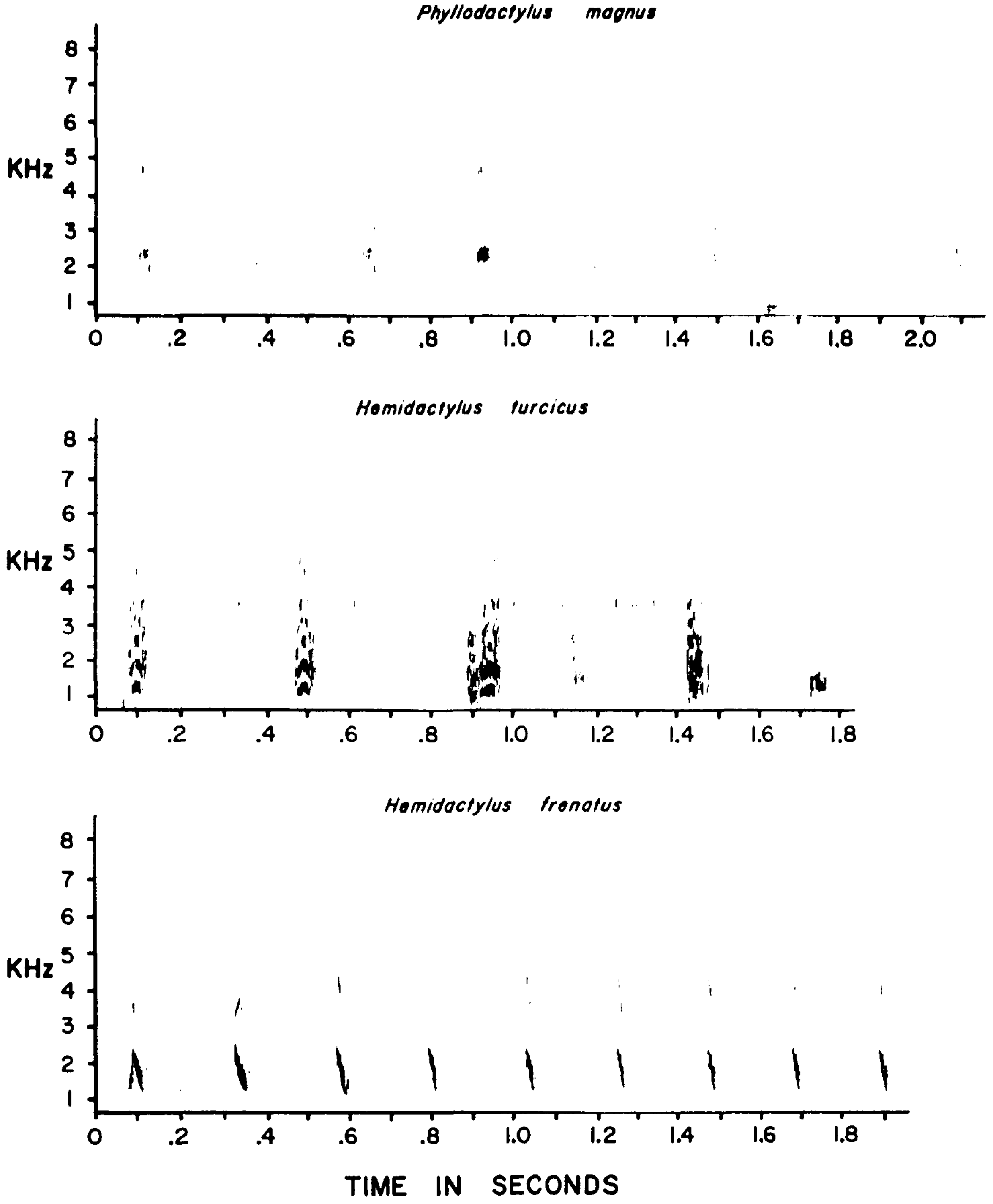


Fig. 21. Sonagrams of the multiple chirp call of the Mexican geckos Phyllodactylus magnus, Hemidactylus turcicus, and Hemidactylus frenatus recorded during 1968 and 1969.

of the chirps are all apparent. The vocalization of *H. turcicus* has longer pauses and a concomitant lower call rate than either of the other two calls. In *H. frenatus* and *H. turcicus* the individual chirps of a call appear to decrease in intensity from first to last. In the call of *P. magnus* the most intense chirps seem to be in the middle of the call. The dominant frequency of the calls is approximately the same, although it appears that *P. magnus* may be slightly higher (2500 Hz). The harmonics for *H. turcicus* seem to be much closer together than those for *H. frenatus*, being at 500 Hz intervals rather than 1500 to 2000 Hz intervals. The pitch of the dominant frequency in each chirp rises and then descends over a range of a few hundred Hz in *H. turcicus*, while in *H. frenatus* it drops 500 to 1000 Hz. This rising and dropping of the pitch, and the relatively close harmonics gives the *H. turcicus* chirps a herring bone effect. The poor resolution of the chirps of *P. magnus* does not permit accurate frequency comparisons.

Although the calls of these three species appear to differ in many respects, it would be presumptuous to postulate species-specific calls on the basis of these limited observations. More data dealing with the vocalizations are required in order that the degree of variation between populations, subspecies, and species can be determined quantitatively. If this is done, it is possible that acoustic behavior can be utilized in conjunction with other evidence to solve many of the taxonomic problems in the family Gekkonidae.

CHAPTER VI

FUNCTIONAL SIGNIFICANCE OF THE MULTIPLE CHIRP CALL

Introduction

Experimental investigations with non-gekkonid lizards and anuran amphibians have elucidated some of the functional aspects of displays (Bogert, 1947; Hunsaker, 1962; Jonsson, 1969; Martof and Thompson, 1958). These authors concluded that the displays can act in territorial behavior, and as ethological isolating mechanisms.

Speculations in the literature concerning the functional significance of gecko acoustic displays, and the contextual judgements concerning call functions in the present study require experimental substantiation. However, no experimental studies have been attempted to explore the functional significance of gecko calls.

Before the experimental work is discussed the question of the ability of geckos to hear their vocalizations will be considered. This question has been partially answered by the work of Wever and his co-workers at Princeton (Peterson, 1966; Wever et al., 1963a,b; 1964, 1965, 1966; Wever and Hepp-Reymond, 1967), and by the recent work of Campbell (1969). By measurement of cochlear potentials the gecko ear has been found to be generally less sensitive to sounds than mammalian ears, but it is as sensitive within a narrow range as a typical mammalian ear (Peterson, 1966). The frequency of greatest sensitivity varied from 100 to 3000 Hz (Campbell, 1969; Wever et al., 1964). Two species of *Hemidactylus* (*H. turcicus* and *H. brookii*) were most sensitive from 100 to 1000 Hz (Wever et al., 1964). The dominant frequencies of the calls of the gecko species studied were between 500 and 3000 Hz (Campbell, 1969 and the present study), strongly suggesting that geckos can hear their own vocalizations.

Materials and Methods

Experimental apparatus

A 12 X 2 X 2 foot rectangular terrarium (Fig. 22) was constructed of an angle iron frame, glass panel front wall, sliding screen doors on top, masonite back wall, and 3/8 inch plywood ends. The floor was covered to a depth of one inch with fine sand, while the back and end walls were covered with a 1/2 inch thick polyfoam pad to reduce sound reflections.

During the experiments the only light was provided by two 10 inch black lights (Blacklight Specialities, Oklahoma City, Okla.) placed on top of the terrarium three feet from either end. The experimental animals were marked with orange radiant flourescent paint (Radiant Color Co.,

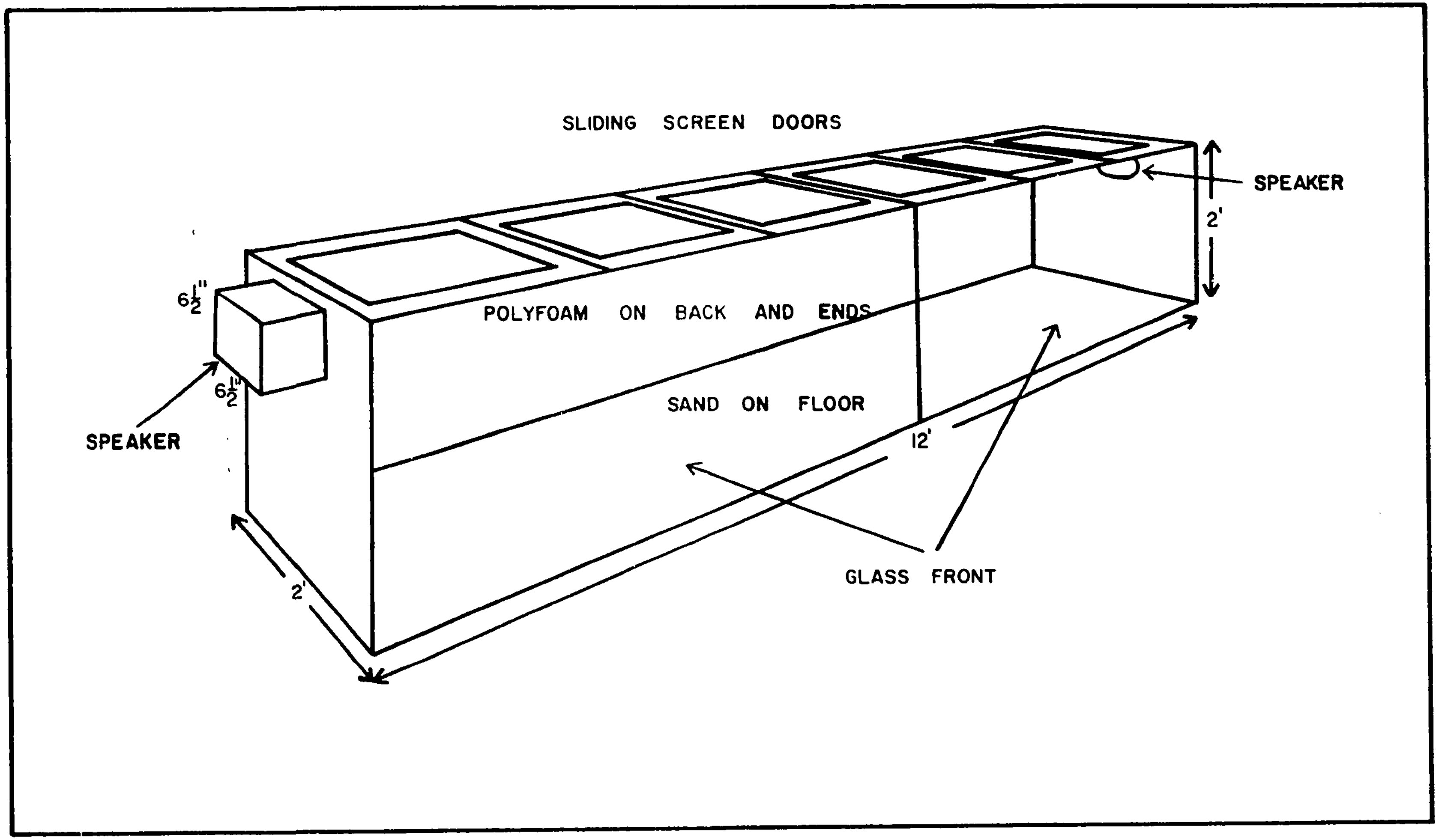


Fig. 22. Experimental terrarium.

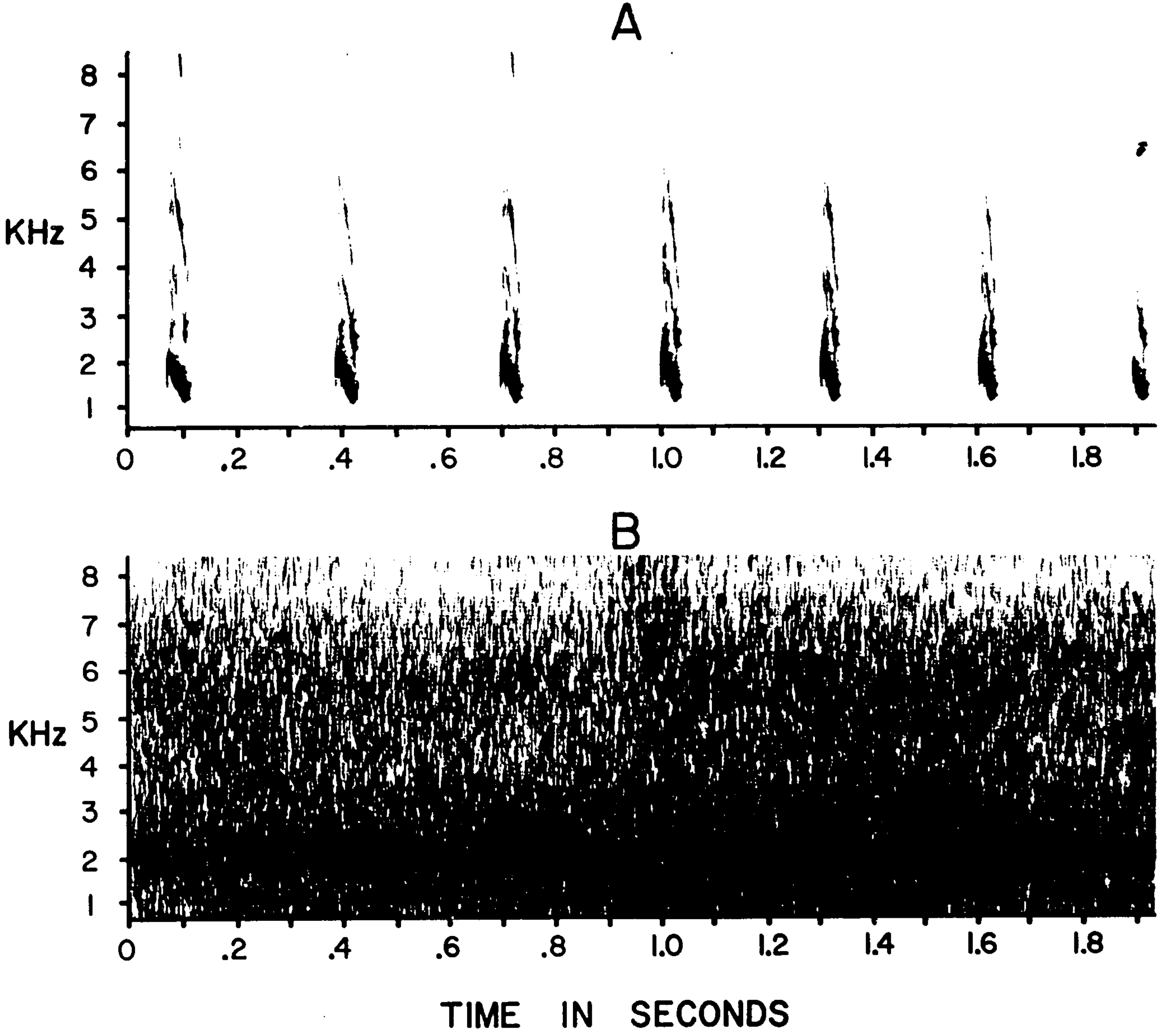
Richmond, Calif.). This paint fluoresces under black light enabling the observer to see the animals under the dim light conditions of the experiments. Observations were made from a 4 X 4 X 5 foot blind placed directly in front of the terrarium.

Two five inch 8 ohm high compliance loudspeakers were mounted, one inch from the top in the center, at either end of the terrarium. The speakers were enclosed in 6½ inch square boxes constructed of ½ inch plywood, and could be individually connected to a Uher 4000 Report L tape recorder within the blind.

The vocalization used in the experiments was a multiple chirp call produced by a solitary captive adult male *H. frenatus* (Fig. 23A). The call had been recorded in a small, 12 X 12 X 18 inch wire mesh cage at an ambient temperature of approximately 27 C, and was loud, clear and nearly two seconds in duration. A 30 minute experimental tape was made by duplicating the call at one minute intervals.

The other taped sound used in the experiments was that of white noise (Fig. 23B). This was obtained by tuning an F.M. radio between stations and recording the resultant noise. In the absence of a white noise generator this is a recognized method of obtaining a sound that contains all frequencies in nearly equal measure (H. Frings, personal communication). A two second segment of noise was

Fig. 23. Sonagrams of a male multiple chirp call (A) and a white noise (B) used in choice experiments testing the functional significance of the male *Hemidactylus frenatus* multiple chirp call.


A
B
KHz
1
2
3
4
5
6
7
8
0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
TIME IN SECONDS

duplicated at one minute intervals to produce a 30 minute experimental tape. Both experimental tapes were recorded with the same equipment as described in Chapter V.

Experimental animals

The twenty adult H. frenatus of each sex used in the experiments were obtained from the population at the Hotel Valles, Ciudad Valles, S.L.P., Mexico in August (Aug. 23-26) of 1969. The sexes were held separately and males were kept individually in small (8 in by 3 in diameter) circular cardboard containers. Females were maintained five to a cage in 12 X 12 X 18 inch wire-mesh cages. It is felt that this means of holding the animals reduced individual interactions and prevented the formation of aberrant social structures which might have affected the experimental results. Meal worm larvae and water were provided ad libitum, and most of the animals remained vigorous during the month of experimentation. Deaths and escapes during the experimental period reduced the numbers of males and females to 18 and 15 at the conclusion of the experiments.

Experimental procedures

Tests were run in October of 1969 at the University of Oklahoma Animal Behavior Laboratory. Work generally began at dusk (8:30 PM) and continued until 10:00 or 11:00 PM. Air temperature during the experiments varied from 25 to 28 C with an average of 27 C. The experimental animal was placed under an opaque glass release jar in the center back of the terrarium, and the experimental tape played over one of the speakers for a 5 min period. The volume of the recording 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 off the animal by a string from inside the blind. As the tape continued to play, the gecko was allowed 30 min to reach the wall at either end of the enclosure. Reaching the end wall constituted a choice, and the trial was terminated. If the animal did not reach one of the end walls within 30 min the trial was scored no choice. The animals were run, one after another, for two trials alternating the speakers used regardless of previous results. Thus, each animal had two trials, one from each speaker, in each experiment.

Three separate experiments were performed following the procedure outlined above. 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 21. In trial one, 7 females chose the end wall where the call was being played, while 4 chose the opposite wall. This 1.75 : 1 ratio (females toward call) was found to be non-significant by a Chi-square test. The second trial reversed the trend with more females moving away from the call (2:1 away) and was also non-significant. The combined results for trial 1 and 2 produced an almost perfect 1:1 ratio, strongly indicating that the choices of the females are at random.

Table 21. Responses of female Hemidactylus frenatus to a recorded male call with statistical evaluation of results.

Trial	Responses			Chi-square Values	Chi-square Probabilities
	Toward	Away	No Choice		
1	7	4	8	0.82	P 0.50 = 0.455 P 0.10 = 2.706
2	4	8	6	1.34	same
1+2	11	12	14	0.04	P 0.90 = 0.016 P 0.50 = 0.455

The upper part of Table 22 shows the responses of male H. frenatus to the male multiple chirp call. In the initial trial 12 males moved away from the end at which the call was being played while 4 moved to the call end. The resultant 3:1 ratio was statistically significant at the 5% level. Trial 2 also resulted in more males moving away from the side of the acoustic display (2:1) but the ratio was not statistically significant. The combined results produce a 2.4 : 1 ratio and these data are significant at the 2.5% level.

It appeared from the data presented above that male

Table 22. Responses of male *Hemidactylus frenatus* to a recorded male call and to white noise with statistical evaluation of results.

Experiment	Responses			Chi-square Values	Chi-square Probabilities
Male call	Toward	Away	No choice		
Trial 1	4	12	2	4.00*	P 0.05 =3.841 P 0.025=5.024
Trial 2	6	12		2.00	P 0.50 =0.455 P 0.10 =2.706
1+2	10	24	2	5.76*	P 0.025=5.024 P 0.01 =6.635
White noise	Toward	Away	No choice		
Trial 1	6	8	3	0.14	P 0.90 =0.016 P 0.50 =0.455
Trial 2	6	7	2	0.08	same
1+2	12	15	5	0.17	same

* Significant deviation from expected

H. *frenatus* were repelled by a male multiple chirp call. However, it is possible that the geckos were merely avoiding the noise rather than the call. To test this idea a white noise of similar duration to the call was played to the male geckos. The results of this experiment are shown in the lower half of Table 22. In both trials, and the combined trials, a ratio of approximately 1:1 was obtained. This ratio indicates no directed response to the white noise.

The males and females in Tables 21 and 22 not only differed in response to a male call, but also in numbers of animals making no choice. Fourteen of 37 female trials resulted in no choice while only 7 of 61 males made no choise.

The possibility that the lizards' choices are being affected by some factor within the terrarium was checked by tallying the number of times the left and right ends were chosen. The right end was chosen 47 times and the left 40 times. A Chi-square value of 0.56 (P 0.50 = 0.46, P 0.30 = 1.07) 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

The females apparently made no directed response to the male multiple chirp call, and in fact, seemed weakly stimulated to move. In the light of results from similar experiments of this type with diurnal lizards and anuran amphibians it was thought that the females would be attracted to the male calls. In diurnal lizards with visual displays this has proved to be the case. Hunsaker (1962) observed that females of the Sceloporus torquatus group of lizards preferentially associated with models performing the display of the female's species. Jensson (1969), working with Anolis nebulosus, demonstrated that females were attracted to a filmed species-specific display. Both of these authors suggest that the male display could serve as an ethological isolating mechanism in areas of closely related sympatric species.

The sounds of males may attract females in anurans. Bogert (1947) in an experimental study of the responses of Bufo terrestris to recordings of the male call noted that females were attracted. Martof and Thompson (1958) observed that recordings of breeding calls of Pseudacris nigrita attracted gravid females of the species. Awbrey (1965) tested several anurans, in both choice and no choice situations, and his results indicate that breeding calls attract females. These authors all point out that the calls could function as ethological isolating mechanisms between closely related sympatric populations.

In the present study there are at least two factors which might have resulted in the lack of female response to a male call. First, the experimental call may not have been the proper stimulus for female attraction. Although the multiple chirp call appeared to be the most likely choice for such experimentation, it is possible that another call functions as a breeding call. Further, it is possible that more than one call has been lumped under the name of multiple chirp call, and the call utilized in the experiment does not function to attract females. Second, the physiological state of the females varied. They were not in the same stage of estrous, and a few were gravid. Physiological state is known to affect the behavior of lizards (Ferguson, 1966) and may be responsible for the inconclusive results in the present study.

In general, males gave a negative response to the male multiple chirp call and were more stimulated to move than females. Further it was determined that their behavior was not merely an avoidance of noise but an avoidance of the vocalization.

Experimental studies dealing with male responses to displays in diurnal lizards have been few in number. Harris (1964) constructed a wooden model of Agama agama which could be made to display by pulling a string. This simulated lizard elicited strong aggressive reactions from nearby males. Jenssen (1969) presented male 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 calls of male anurans have been shown to repel conspecific males. Duellman (1966) has described vocalizations of male dendorbatid frogs that serve to keep other males away. Bogert (1947) in his experiments with <u>Bufo terrestris</u> noted that males were repelled by male breeding calls. The recent 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.

The investigations above, and the present study, provide evidence that the vocal displays of male geckos could function to establish and maintain territories. The selective advantage of these territorial vocalizations are obvious. By promoting territoriality, they tend to organize and space out the population, and 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. The males can, for the most part, maintain their territories merely by informing other males of their presence by a vocal display.

It should be stressed that the results obtained in this study are preliminary and that much more work must be done before definitive statements can be made concerning the function of the multiple chirp call in *H. frenatus*.

CHAPTER VII

SUMMARY

The present study is the first ethoecological work done with Hemidactylus frenatus, and the first detailed study of any member of the genus in the New World. The study had its inception in May 1968 and continued through September 1969. Over 300 H. frenatus from a population at the Hotel Valles in Ciudad Valles, San Luis Potosí, Mexico were studied in the field (March-May 1969) and in the laboratory (October 1969). Ecology and behavior were described with emphasis on description and analysis of acoustic behavior. An experimental study of the functional aspects of the vocalizations was also performed. The results of this investigation are summarized below.

H. frenatus has an extremely wide pantropical distribution and can be referred to as a "weedy" species. In Mexico it is found largely on the west coast with only a few eastern slope collecting localities. Distribution is along routes of commerce and the species is found almost entirely within human settlements.

The climate of Ciudad Valles is tropical with relatively high temperatures much of the year (mean 20 to

25 C). Rain falls in every month with a maximum during the summer months. Daily temperature and humidity changes are gradual with highest temperature - lowest humidity occurring the the afternoon, and lowest temperature - highest humidity in the early morning hours.

The sex ratio is biased in favor of females (45:55) and this result agrees with other gecko studies. The greater activity of males, resulting in higher predation, appears to be the cause of the unbalanced sex ratio.

The sexes differ significantly in size, with males being longer and heavier than females. The average snout-vent length and weight of males were 51.0 mm and 3.2 gm while the length and weight of females averaged 50.0 mm and 2.9 gm respectively. Distinct size classes due to age are obscured in the population because the geckos are long-lived, reach adult size in a year, and have an extended breeding season.

Calculated growth rates fit the classic idea of animal growth with very rapid growth at first (4.4 mm per month) and a slowing as maturity is reached (.97 mm per month). A significant sexual difference in growth rate was found in the largest size class. The growth rate of females slows more rapidly than that of males as maturity is approached.

The tail is approximately equal in length to the body (1:1). In males the tail is shorter in adults than in young, but in females the opposite is the case. Geckos differ from most other lizards in having tails which are equal to or shorter than their bodies.

Evidence of natural tail breakage was found in nearly 40% of the animals collected. Smaller animals have a lower frequency of broken tails than larger animals, and females have a lower incidence of breakage than males. Tail breakage probably occurs during conspecific aggressive interactions and as a result of unsuccessful predation.

Shedding geckos can not cling to vertical surfaces or ceilings and are secretive and quiescent during ecdysis.

A population density of 6200 individuals per acre, and a biomass of 18,600 grams per acre were calculated for *H. frenatus*. Density and biomass were found to be affected by the nature of the habitat. The biomass and density of *H. frenatus* are high compared to other species of lizards. It was concluded that the high figures were due to the multiple dimensions of the geckos' habitat.

Cloacal temperatures of active geckos ranged from 19.0 to 34.3 C with a mean of 27.2 C. Cloacal temperatures are closely correlated with air, and especially with substrate temperatures. However, body temperatures are usually higher than environmental temperatures due to limited thermoregulatory behavior. Cloacal temperatures of *H. frenatus* are lower and much more variable than those of diurnal lizards. It was suggested that the term "mean activity temperature" be substituted for "mean preferred temperature" in studies of nocturnal gecko thermal ecology.

Annual periodicity in H. frenatus is probably dependent on temperature. Gecko activity increased over the three month study period, and the increase was closely correlated with rising temperatures. There was a greater correlation between number of active geckos and diurnal temperatures than between activity and nocturnal temperatures. Diel activity demonstrated that the geckos are almost exclusively nocturnal and that the determinate for initiation and cessation of activity is light. Nocturnal activity increases from dusk to a high at 1:00 AM, and is maintained at about this level until dawn. Nocturnal activity can be reduced by factors such as human activity, wind, rain, and low temperature.

Habitat preference was determined; geckos prefer large complex structures with some artificial light. Concentrations of animals occur in areas with adequate places of refuge, dim artificial light, and low levels of human activity. Perch sites are generally high (3.0 m), on wood, and vertical, with height and vertical orientation being the most important factors.

The average distance between captures for Main Building animals was 2.7 ± 2.14 m and 3.9 ± 2.74 m for males and females respectively. The average distance between captures for Doña María males and females was 7.2 ± 4.48 m and 3.8 ± 3.62 m. Building differences in movement are statistically significant, and are related to differences in building population density. Average distance between captures increases with increasing body length in males, but not in females. Male increase in movement with size is thought to be due to increasing dominance and aggressiveness of large males.

Two types of territoriality are found in adult male H. frenatus. Some individuals exhibit classic territoriality and defend a given area from conspecific males. Other animals seem to have dynamic territories that move with them.

The breeding structure of the gecko population is a type of limited polygamy. Groups of geckos generally consist of one, or infrequently two, adult males, two or more adult females, and varying numbers of subadults of both sexes. This differs from the breeding structure of non-gekkonid lizard populations which generally exhibit a type of facultative monogamy.

The estimated breeding cycle for Ciudad Valles H. frenatus is as follows. In February animals emerge from winter retreats and territoriality, male aggression, and mating begin. These activities continue, with egg laying and hatching of young, until cold weather returns in November of December. In the nine month activity season at least three broods per female are possible.

Feeding was observed, and the geckos are opportunistic insectivores. They consume large numbers of small moths, mosquitoes, and leafhoppers, as well as attempting to subdue extremely large food items. Vision plays a predominant role in feeding, and depending on the size of the food item, two types of feeding behavior are observed.

The *locomotion* of *H. frenatus* is similar to that of other quadrupeds, except that the body is kept close to the substrate and sinuous side to side movements of the body accompany locomotion. These modifications may increase frictional contact with the substrate and thus could aid the animal in moving on walls and ceilings.

Two types of *eliminative behavior* were observed that differed in posture depending upon the orientation of the substrate.

Escape behavior consists of immobilizing to escape detection, moving out of sight, and seeking permanent shelter. When caught, tail autotomy, biting and vigorous struggling are utilized to break free.

Animal associates of the geckos are food competitors, such as *Sceloporus variabilis*, and predators, such as house cats.

Courtship and copulation were observed and were divided into five stages on the basis of male behavior (approach, initial hold, neck hold, copulation, and post copulation). Courtship in H. frenatus, and in other nocturnal geckos studied, differs from that of diurnal lizards in that geckos perform no displays prior to mating. Contact seems to be the first essential element in nocturnal gecko mating.

The tail wag was a commonly observed behavior that is used in a variety of asocial and social contexts. In all cases it occurred at moments of high nervous tension.

Aggressive behavior is exhibited only by males and is of two types. The first type is a low intensity encounter which is quite common and involves no special posture or display. The second type is infrequently observed, and is of high intensity. These high intensity encounters always involve adult males that vocalize, posture, and occasionally fight. Nocturnal geckos appear to possess the same facets of aggressive behavior as other lizards, except that displays are auditory as well as visual.

Contextual observations and recordings of vocalizations demonstrate at least three functionally, and physically, distinct types of calls. These are the multiple chirp, the churr and the single chirp calls.

The multiple chirp call is the most commonly heard vocalization and is closely associated with agonistic behavior and territoriality. The call consists of a series of loud chirps (average 9) that are suggestive of the barking of a small dog. Sonagraphic analysis of the chirps shows a dominant frequency of approximately 2000 Hz and a frequency range from below 1000 to over 14,000 Hz. The mean call rate is 4.51 chirps per second. A highly significant positive correlation exists between call rate and temperature. The call is found to have a highly consistent temporal pattern.

Calling periodicity was investigated for the multiple chirp call. The average daily number of calls for each week of the study was found to increase over the three month study period. Average number of calls per week was closely correlated with average numbers of geckos censused, and both were correlated with average weekly temperature data. Twenty-four hour calling periodicity was determined and calls were observed to increase from dusk to a high in the early morning hours. The number of calls per hour is correlated with the number of active geckos. The limits of vocal activity are determined by light intensity with few calls before dusk and after dawn.

The *churr call* was infrequently heard, occurring only during high intensity aggressive encounters. This call probably functions as a last moment warning or intimidation. The churr is a rapid series of short chirps lasting less than 0.2 of a second. The dominant frequency of the chirps is approximately 2000 Hz.

The *single chirp call* was frequently heard and is closely associated with distress. This call occurs during rough handling and aggressive encounters. The chirp is a single, short (.05 of a second) sound with a dominant frequency of 2000 Hz.

In order to elucidate possible species-specific differences in the multiple chirp call, a comparison was made between the calls of *Hemidactylus frenatus*, *H. turcicus* and *Phyllodactylus magnus*. The calls differ in physical as well as temporal aspects, and could possibly be species-specific.

The functional significance of the multiple chirp call was investigated by experimental means. A male call was played to male and female *H. frenatus* in a choice situation. Females made no directed response to the male call. Males gave a significant negative response to the call, and it was determined that this was not merely an avoidance of noise but an avoidance of the vocalization. These results provide evidence that the vocal displays of male geckos could function in establishment and maintenance of territories.

LITERATURE CITED

Andrewartha, H.G. 1961. Introduction to the study of animal populations. Univ. of Chicago Press, Chicago. 281 p.

Auffenberg, W. 1965. Sex and species discrimination in two sympatric South American tortoises. Copeia 1965: 335-342.

Awbrey, E.T. 1965. An experimental investigation of the effectiveness of anuran mating calls as isolating mechanisms. Ph.D. Thesis. Univ. Texas.

Barwick, R.E. 1959. Life history of the common New Zealand skink *Leiolopisma zelandica*. Trans. Roy. Soc. N.Z. 86: 331-380.

Beebe, W. 1944. Field notes on the lizards of Kartabo, British Guiana, Caripito, Venezuela. Part 1. Gekkonidae. Zoologica 29: 145-160.

Bellairs, A.d'A. 1957. Reptiles. Hutchinson's Univ. Library. London.

Blair, W.F. 1958. Call difference as an isolation mechanism in Florida species of hylid frogs. Quart. J. Fla. Acad. Sci. 21: 32-48.

________. 1960. The rusty lizard. Univ. of Texas Press, Austin, Texas. 185 p.

________. 1963. Acoustic behavior of Amphibia, p. 694-708. *In* R.-G. Busnel (ed.) Acoustic behaviour of animals. Elsevier Pub. Co., New York. 933 p.

________. 1968. Amphibians and reptiles, p. 289-311. *In* T.A. Sebeok (ed.) Animal communication. Indiana Univ. Press, Bloomington, Indiana. 686 p.

Blanford, W.T. 1876. Eastern Persia. Vol. II. The zoology and geology. MacMillan, London.

Bogert, C.M. 1947. A field study of homing in the Carolina toad. Amer. Mus. Novitates 1355: 1-24.

________. 1949. Thermoregulation in reptiles: a factor in evolution. Evolution 3: 195-211.

________. 1960. The influence of sound on the behavior of amphibians and reptiles, p. 137-321. In W.E. Lanyon and W.N. Tavolga (ed.) Animal sounds and communication. Publ. No. 7 Amer. Inst. of Biol. Sci., Washington 6, D.C. 443 p.

Boulenger, G. 1885. Catalogue of the lizards in the British Museum (Natural History). 2nd ed., London: Taylor and Francis 1: 1-436.

Brain, C.K. 1962. A review of the gecko genus Ptenopus with the description of a new species. Cimbebasia 1: 1-18.

Brattstrom, B.H. 1965. Body temperatures of reptiles. Amer. Midl. Natur. 73: 376-422.

Broughton, W.B. 1963. Method in bioacoustic terminology, p. 3-25. In R.-G. Busnel (ed.) Acoustic behaviour of animals. Elsevier Pub. Co., New York. 933 p.

Bustard, H.R. 1964. Defensive beahvior shown by Australian geckos, genus Diplodactylus. Herpetologica 20: 198-200.

________. 1967a. Activity cycle and thermoregulation in the Australian gecko Gehyra variegata. Copeia 1967: 753-758.

________. 1967b. Defensive display behavior of the Australian gecko Nephrurus asper. Herpetologica 23: 126-129.

________. 1968a. The ecology of the Australian gecko, Gehyra variegata in New South Wales. J. Zool., Lond. 154: 113-138.

________. 1968b. The ecology of the Australian gecko Heteronotia binoei in northern New South Wales. J. Zool., Lond. 156: 483-497.

Cagle, F.R. 1946a. A lizard population on Tinian. Copeia 1946: 4-9.

________. 1946b. Tail loss and regeneration in a Pacific island gecko. Copeia 1946: 45.

Camp, C.L. 1923. Classification of the lizards. Amer. Mus. Natur. Hist. 48: 289-481.

Campbell, H.W. 1969. The effects of temperature on the auditory sensitivity of lizards. Physiol. Zool. 42: 183-211.

Capranica, R.R. 1968. The vocal repertorie of the bullfrog (*Rana catesbeiana*). Behaviour 31: 302-325.

Carpenter, C.C. 1963. Patterns of behavior in three forms of the fringe-toed lizards (*Uma* - Iguanidae). Copeia 1963: 406-412.

________. 1964. Comparative behavior of the lava lizards (*Tropidurus*) of the Galapagos Islands. Symposium paper presented to the Galapagos International Scientific Project aboard the Golden Bear in January, 1964.

________. 1967. Aggression and social structure in iguanid lizards, p. 87-105. *In* W.W. Milstead (ed.) Lizard ecology: a symposium. Univ. Missouri Press, Columbia. 300 p.

Church, G. 1962. The reproductive cycles of the Javanese house geckos, *Cosymbotus platyurus*, *Hemidactylus frenatus*, and *Peropus mutilatus*. Copeia 1962: 262-269.

Church, G., and L. Chun-Sim. 1961. The distribution of three species of house gecko in Bandung (Java). Herpetologica 17: 199-201.

Clark, R.F. 1965. An ethological study of the iguanid genera *Callisaurus*, *Cophosaurus* and *Holbrookia*. Emporia State Res. Stud. 13: 1-66.

Cockrum, R.E. 1962. Introduction to mammalogy. Ronald Press Co., New York. 455 p.

Cowles, R.E., and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Amer. Mus. of Natur. Hist. 83: 265-295.

Darlington, P.J. 1957. Zoogeography. John Wiley & Sons, New York. 675 p.

DeSola, R. 1930. The Liebespiel of *Testudo vandenburghi* a new name for the Mid-Albermarle Island Galapagos tortoise. Copeia 1930: 79-80.

Dixon, J.R. 1964. Further data on the geckos (Phyllodactylus) of islands in the extreme southern Caribbean. Southwest. Natur. 9: 203-205.

Duellman, W.E. 1966. Aggressive behavior in dendrobatid frogs. Herpetologica 22: 217-221.

Dumortier, B. 1963. Ethological and physiological study of sound emissions in Arthropoda, p. 583-649. In R.-G. Busnel (ed.) Acoustic behaviour of animals. Elsevier Pub. Co., New York. 933 p.

Emlen, S.T. 1968. Territoriality in the bullfrog, Rana catesbeiana. Copeia 2: 240-243.

Evans, L.T. 1936. The development of the cochlea in the gecko, with special reference to the cochlea-lagena ratio and its bearing on vocality and social behavior. Anat. Rec. 64: 187-201.

________. 1961. Structure as related to behavior in the organization of populations in reptiles. In W.F. Blair (ed.) Vertebrate speciation. Univ. Texas Press, Austin, Texas.

Ferguson, G.W. 1966. Effect of follicle stimulating hormone and testosterone propionate on reproduction of the side blotched lizard, Uta stansburiana. Copeia 1966: 495-498.

________. 1969. Geographic variation and evolution of stereotyped behavioral patterns of the side-blotched lizards of the genus Uta (Iguanidae). Ph.D. Thesis. Univ. Michigan. 95 p.

Fitch, H.S. 1964. The life history and ecology of the five-lined skink Eumeces fasciatus. Univ. Kansas Mus. Natur. Hist. Misc. Publ. 8: 1-156.

________. 1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. Univ. Kansas Publ. Mus. Natur. Hist. 8: 417-476.

________. 1958. Natural history of the six-lined racerunner (Cnemidophorus sexlineatus). Univ. Kansas Publ. Mus. Natur. Hist. 11: 11-62.

Frings, H. and M. Frings. 1962. Effects of temperature on the ordinary song of the common meadow grasshopper, Orchelimum vulgare (Orthoptera: Tettigoniidae). J. Exp. Zool. 151: 33-51.

Fry, F.E. 1967. Responses of vertebrate poikilotherms to temperature, p. 375-459. In A.H. Rose (ed.) Thermobiology. Academic Press, New York. 635 p.

Gennaro, J.F. Jr. 1969. The gecko grip. Natur. Hist. 77: 36-42.

Greenberg, B. 1943. Social behavior of the western banded gecko, Coleonyx variegatus Baird. Physiol. Zool. 16: 110-122.

Greer, A.E. 1967. The ecology and behavior of two sympatric Lygodactylus geckos. Breviora 268: 1-19.

Hardy, D.F. 1962. Ecology and behavior of the six-lined race runner Cnemidophorus sexlineatus. Univ. Kansas Sci. Bull. 43: 3-73.

Harris, V.A. 1964. The life of the rainbow lizard. Hutchinson Trop. Monogr., Hutchinson and Co., Ltd., London. 174 p.

Heatwole, H. 1966. Factors affecting orientation and habitat selection in some geckos. Zeitschr. Tierpsychol. 23: 303-314.

Heatwole, H., and O.J. Sexton. 1966. Herpetofaunal comparisons between two climatic zones in Panama. Amer. Midl. Natur. 75: 45-60.

Hinde, R.A., and N. Tinbergen. 1958. The comparative study of species-specific behavior, p. 251-268. In A. Roe and G.G. Simpson (ed.) Behavior and evolution. Yale Univ. Press, New Haven.

Hirth, H.F. 1963. The ecology of two lizards on a tropical beach. Ecol. Monogr. 33: 83-112.

Hunsaker, D. 1962. Ethological isolating mechanisms in the Sceloporus torquatus group of lizards. Evolution 16: 62-74.

Inger, R.F. 1959. Temperature responses and ecological relations of two Bornean lizards. Ecology 40: 127-136.

Jenssen, T.A. 1969. Ethoecology and display analysis of Anolis nebulosus (Sauria, Iguanidae). Ph.D. Thesis. Univ. Oklahoma. 235 p.

Jorgenson, C.O., and W.W. Tanner. 1963. The application of the density probability function to determine the home ranges of *Uta stansburiana* and *Cnemidophorous tigris*. Herpetologica 19: 105-115.

Kastle, W. 1964. Verhaltensstudien an Taggeckonen der Gattungen *Lygodactylus* und *Phelsuma*. Zeitschr. Tierpsychol. 21: 486-507.

King, W. 1959. Observations on the ecology of a new population of the mediterranean gecko, *Hemidactylus turcicus* in Florida. Quart. J. Fla. Acad. Sci. 21: 317-318.

Kluge, A.G. 1962. Comparative osteology of the eublepharid lizard genus *Coleonyx* Gray. J. Morph. 110: 299-332.

________. 1964. A revision of the South American gekkonid lizard genus *Homonota* Gray. Amer. Mus. Novitates 2193: 1-472.

________. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. Bull. Amer. Mus. Natur. Hist. 135: 1-60.

________. 1969. The evolution and geographical origin of the new world *Hemidactylus mabouia* - *brookii* complex (Gekkonidae, Sauria). Misc. Publ. Mus. Zool. Univ. Michigan 138: 78 p.

Leopold, A.S. 1950. Vegetation zones of Mexico. Ecology 31: 507-518.

Licht, P., W.R. Dawson, V.H. Shoemaker, and A.R. Main. 1966 a. Observations on thermal relations of western Australian lizards. Copeia 1966: 97-110.

________. 1966b. Heat resistance of some Australian lizards. Copeia 1966: 162-169.

Liner, E.A., and H.A. Dundee. 1969. Notes on reptiles and amphibians from southern Guerrero and Oaxaca, Mexico. Southwest. Natur. 14: 129-134.

Loveridge, A. 1947. Revision of the African lizards of the family Gekkonidae. Bull. Mus. Comp. Zool. 98: 1-469.

Mahendra, B.C. 1936. Contributions to the bionomics, anatomy, reproduction and development of the Indian house-gecko *Hemidactylus flaviviridis* Ruppel. Part I. Proc. Indian Acad. Sci. 4: 250-281.

Mahendra, B.C. 1941. Contributions to the bionomics, anatomy, reproduction and development of the Indian house-gecko, Hemidactylus flaviviridis Ruppel. Part II. Proc. Indian Acad. Sci. 13: 288-306.

Marler, P. 1960. Bird songs and mate selection, p. 348-368. In W.E. Lanyon and W.N. Tavolga (ed.) Animal sounds and communication. Publ. No. 7 Amer. Inst. of Biol. Sci., Washington 6, D.C. 443 p.

Martof, B. 1953. Territorality in the green frog, Rana clamitans. Ecology 34: 529-534.

Martof, B., and E.F. Thompson, Jr. 1958. Reproductive behavior of the chorus frog (Pseudacris nigrita). Behaviour 13: 243-258.

Mayhew, W.W. 1963. Temperature preference in Sceloporus orcutti. Herpetologica 18: 217-233.

Mayr, E. 1958. Behavior and systematics, p. 341-372. In A. Roe and G.G. Simpson (ed.) Behavior and evolution. Yale Univ. Press, New Haven.

Mertens, R. 1955. Die Amphibien und Reptilien Südwest-afrikas. Natur. Ges. 490.

Miller, A. and D.H. Gould. 1951. The extensive cold air outbreak of January 24-31, 1951. Monthly Weather Rev. 79: 20-26.

Mills, R.H., and B.B. Hull. 1949. Weather summary, Mexico; for use with naval air pilots. H.O. Publ. Washington, D.C. 532: 1-220.

Miyamoto, S. 1930. Über Geckonen als Moskitofänger. J. Med. Assoc. Formosa 30: 228.

McIlhenny, E.A. 1935. The alligator's life history. Christopher Publ. House, Boston. 117 p.

Noble, G.K., and H.T. Bradley. 1933. The mating behavior of lizards: its bearing on the theory of sexual selection. Ann. New York Acad. Sci. 35: 25-100.

Odum, E.P. 1959. Fundamentals of ecology. W.B. Saunders Co., Philadelphia. 546 p.

Oliver, J.A. 1955. The natural history of North American amphibians and reptiles. D. Van Nostrand Co. Inc., New Jersey. 359 p.

Park, O. 1938. Studies in nocturnal ecology 7. Preliminary observations on rain forest animals. Ecology 19: 208-223.

Pesman, M.W. 1962. Meet flora Mexicana. Northland Press, Flagstaff, Arizona. 279 p.

Peterson, C.G.J. 1896. The yearly immigration of young plaice into the Limfjord from the German sea. Rept. Danish Biol. Sta. 6(1895): 1-77.

Peterson, E.A. 1966. Hearing in the lizard: some comments on the auditory capacities of a nonmammalian ear. Herpetologica 22: 161-171.

Petzold, H. 1965. On the resistance of gecko eggs and some observations on Hemidactylus frenatus Dum. and Bibr. 1936. Zool. Garten 31: 261-265.

Pope, C.H. 1946. Turtles of the United States and Canada. Alfred A. Knopf Inc., New York. 343 p.

Rand, A.S. 1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45: 745-752.

________. 1967. The adaptive significance of territoriality in iguanid lizards, p. 106-115. In W.W. Milstead (ed.) Lizard ecology: a symposium. Univ. Missouri Press, Columbia. 300 p.

Repenning, C. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic, p. 288-311. In D. Hopkins (ed.) The Bering land bridge. Stanford Univ. Press.

Rose, F.L., and C.D. Barbour. 1968. Ecology and reproductive cycles of the introduced gecko, Hemidactylus turcicus in the southern United States. Amer. Midl. Natur. 79: 159-168.

Ruibal, R. 1961. Thermal relations of five species of tropical lizards. Evolution 15: 98-111.

Schmidt, K.P., and R.F. Inger. 1957. Living reptiles of the world. Doubleday Co., Garden City, New York. 287 p.

Schmidt-Nielsen, K., and W.R. Dawson. 1964. Terrestrial animals in dry heat: desert reptiles, p. 467-492. In D.B. Dill, E.F. Adolph, and C.G. Wilber (ed.) Handbook of physiology, sec. 4. Amer. Physiol. Soc., Washington. 1056 p.

Simpson, G. 1952. Probabilities of dispersal in geologic time. *In* E. Mayr (ed.) The problem of land connections across the south Atlantic, with special reference to the Mesozoic. Bull. Amer. Mus. Natur. Hist. 99: 163-176.

Smith, H.M., and E.H. Taylor. 1950. Annotated checklist and keys to the reptiles of Mexico exclusive of the snakes. Bull. U.S. Natur. Mus. 199: 1-253.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry: The principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco. 776 p.

Soule, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. Copeia 1963: 107-115.

St. Girons, H., and M.C. St. Girons. 1956. Cycle d'activite et thermoregulation chez les reptiles (lezards et serpents). Vie et Milieu 7: 133-226.

Stephenson, N.G. 1960. The comparative osteology of Australian geckos and its bearing on their morphological status. J. Linnean Soc. London, Zool., 279: 278-299.

Tembrock, G. 1963. Acoustic behaviour of mammals, p. 751-789. *In* R.-G. Busnel (ed.) Acoustic behaviour of animals. Elsevier Publ. Co., New York. 933 p.

________. 1968. Land mammals, p. 338-405. *In* T.A. Sebeok (ed.) Animal communication. Indiana Univ. Press., Bloomington. 686 p.

Templeton, J.R. 1960. Respiration and water loss at the higher temperatures in the desert iguana, *Dipsosaurus dorsalis*. Physiol. Zool. 33: 136-145.

Tinkle, D.W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. Mus. Zool., Univ. Michigan, Ann Arbor. 182 p.

Underwood, G. 1954. On the classification and evolution of geckos. Proc. Zool. Soc. Lond. 124: 469-492.

Vivo Escoto, J.A. 1964. Weather and climate of Mexico and Central America, p. 187-215. *In* R.C. West (ed.) Handbook of middle American Indians. Univ. Texas Press, Austin. 545 p.

Watkins, W.A. 1967. The harmonic interval: fact or artifact in spectral analysis of pulse trains, p. 15-43. *In* W.N. Tavolga (ed.) Marine Bio-Acoustics, Vol. 2. Pergamon Press, Oxford. 353 p.

Wermuth, H. 1965. Liste der rezenten Amphibien und Reptilien: Gekkonidae, Pygopodidae, Xantusiidae. Das Tierreich 80: 1-246.

Werner, [illegible] 1961. The vertebral column of the geckos (Gekkonoidea) with special consideration of the tail. Ph.D. Thesis. The Hebrew Univ. of Jerusalem.

________. 1965. Über die israelischen Geckos der Gattung *Ptyodactylus* und ihre Biologie. Zeitschr. fur Herpetologie und Terrarienkunde 1: 15-25.

________. 1968. Regeneration frequencies in geckos of two ecological types. Vie et Milieu 14: 199-222.

Wever, E.G., and E.A. Peterson. 1963. Auditory sensitivity in three iguanid lizards. J. Aud. Res. 3: 205-212.

Wever, E.G., D.E. Crowley, and E.A. Peterson. 1963a. Auditory sensitivity in four species of lizards. J. Aud. Res. 3: 151-157.

________, J.A. Vernon, E.A. Peterson, and D.E. Crowley. 1963b. Auditory responses in the tokay gecko. Proc. Nat. Acad. Sci. 50: 806-811.

________, E.A. Peterson, D.E. Crowley, and J.A. Vernon. 1964. Further studies of hearing in the gekkonid lizards. Proc. Nat. Acad. Sci. 51: 561-567.

________, J.A. Vernon, D.E. Crowley, and E.A. Peterson. 1965. Electrical output of lizard ear: Relation to hair-cell population. Science 150: 1172-1174.

Wever, E.G., and M.-C. Hepp-Reymond, and J.A. Vernon. 1966. Vocalization and hearing in the leopard lizard, Proc. Nat. Acad. Sci. 55: 98-106.

Wever, E.G., and M.-C. Hepp-Reymond. 1967. Auditory sensitivity in the fan-toed gecko, *Ptyodactylus hasselquistii puiseuxi* Boutan. Proc. Nat. Acad. Sci. 57: 681-687.

Wiewandt, T.A. 1969. Vocalization, aggressive behavior, and territoriality in the bullfrog *Rana catesbeiana*. Copeia 1969: 276-285.