ASPECTS OF THE ECOLOGY AND SYSTEMATICS OF THE LIZARDS COLEONYX BREVIS AND COLEONYX RETICULATUS

(LACERTILIA: GEKKONIDAE)

A Thesis

by

BENJAMIN EDWARD DIAL

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Approved as to style and content by:

James R. Dixon
(Chairman of Committee)

James G. Teer
(Head of Department)

(Member)

Brian N. Cain
(Member)

May 1975

ABSTRACT

Aspects of the Ecology and Systematics of the Lizards
Coleonyx brevis and Coleonyx reticulatus
(Lacertilia: Gekkonidae). (May 1975)
Benjamin Edward Dial, B.S., Texas A&M University
Chairman of Advisory Committee: Dr. James R. Dixon

Natural history studies of Coleonyx brevis involved an analysis of the reproductive and thermal ecology, diet composition, and behavior of the species. Data on the thermal ecology, diet composition, and behavior of a sympatric species, Coleonyx reticulatus, were used on a comparative basis. Several aspects of the ecology of each species allowed for hypotheses to be drawn regarding the mechanics of niche separation between the two species. Squamative and mensural data from each species were recorded and geographic variation in C. brevis was analyzed.

The reproductive cycle of C. brevis involves cyclic gonadal development in males and females. Males emerge from hibernation with enlarged testes and volumes of testes increase until maximum size is attained in April and May. Testes remain enlarged until June, and testes decrease in size in July and August. Females emerge from hibernation with small, unyolked follicles that enlarge quickly, yolk deposition occurs, and ovulation follows. First mating occurs in April and eggs are laid from late May to early

August. Males reach sexual maturity at 45 mm and females at 48 mm. The reproductive strategy of the species was defined by considering four characteristics: number of clutches per season, age at sexual maturity, longevity, and risks taken during reproductive activity. From these, the species is defined as being more K than r-selected.

The diel thermal ecology of *C. brevis* was described by considering field and laboratory temperature data. In the field, environmental and cloacal temperatures were recorded for specimens under cover in the daytime and specimens active at night. In the laboratory, specimens were tested for thermoregulatory behavior; cloacal, cover, and substrate temperatures were recorded. Field and laboratory data reveal that during the daytime *C. brevis* behaviorally thermoregulates by elevating its body into contact with cover items, positioning its body intermediate between cover items and substrate, and lowering its body into contact with substrate. Field data indicate that *C. brevis* thermoregulates by contact with the air and substrate at night. In the laboratory, *C. brevis* and *C. reticulatus* were tested for temperature preferences in a thermal gradient. Data reveal significant differences in temperature preferences, suggesting a temporal difference in activity patterns between the two species.

Stomachs of *C. brevis* were examined and it was concluded that the species is a "fine-grained," opportunistic feeder; 29 families of invertebrates were consumed, most of which were small (average volume-0.01 cc). Three stomachs and two defecations of C. reticulatus revealed that spiders, beetles, and grasshoppers were eaten.

Several aspects of the behavior of each species were studied including exploratory behavior, walking, digging, aggregation, climbing, defensive behavior, territoriality, feeding, and interspecific interference. Laboratory data suggest that C. reticulatus is partially arboreal. Laboratory tests reveal that C. brevis utilizes both chemical and visual cues in feeding.

The methods by which niche separation occurs between the two species may involve reduced competition by: differences in microhabitats utilized (arboreality in one species), temporal differences in activity, and increased differences in snout-vent lengths of each species when they occur sympatrically.

Geographic variation in C. brevis was investigated. Squamative data on C. reticulatus is included in tabular form. A univariate statistical analysis of squamative characters of C. brevis indicates the presence of north-south and/or east-west clines for six of twelve characters. Generally, univariate analysis reveals that populations separate into three major groups.

A multivariate analysis of variance indicates that populations separate into five groups. However, such groups may be considered subgroups of the univariate groups. Generally, the

multivariate analysis lends support to the univariate analysis.

The zoogeography of each species is discussed. Most information consists of a synthesis of theories presented by several authors. However, the present day (relict) distribution of *C. reticulatus* is discussed with regards to its ancestry and certain ecological characters.

ACKNOWLEDGMENTS

Many individuals have contributed considerably to various aspects of this study. I am grateful to members of my graduate advisory committee (Drs. J.R. Dixon and B.C. Cain, Department of Wildlife and Fisheries Sciences, Dr. L.S. Dillon, Department of Biology) for their suggestions and critical review of the thesis. I am particularly indebted to Dr. James R. Dixon for his resourceful advice and encouragement. I appreciate the patience and understanding he has shown; his friendship will always be valued.

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DEDICATION

to Charles L. Simmons

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INTRODUCTION

Systematics, originally thought of as being singularly taxonomic, ultimately includes ecological, ethological, physiological, cytological, biochemical, morphological, and all inheritable characteristics of organisms. It is defined as the scientific study of the kinds of organisms, their diversity, and any and all relationships between them. Thus, all characteristics (life historical, behavioral, functional, and structural) should be considered in interpreting relationships of organisms. For instance, modern students have found that phylogenetically related forms demonstrate homologous behavioral patterns. Likewise, ecological similarities are useful in detecting homology.

Reptiles have been used frequently to express and document ecological and evolutionary theory. Lizard populations in particular lend themselves well to the study of population dynamics, general natural history, and geographic morphological variation. Species that have rapid maturity and short life spans, with the accompanying potential for rapid genetic change, are ideal as field and laboratory subjects.

Certain groups of lizards, such as the iguanids, have been studied quite thoroughly, but comparatively little information is

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The citations and format of this thesis follow the style of the journal Herpetologica.

available for gekkonid lizards; for instance, most members of the subfamily Eublepharinae are poorly known. The subfamily Eublepharinae is the most primitive group of the primitive lizard family Gekkonidae (Kluge, 1967). *Coleonyx* is the only New World representative of the subfamily. Within the genus two types of geckos (with and without tubercles) exist. *Coleonyx brevis* Stejneger, a common species of desert areas, is a representative of the non-tubercular form and *Coleonyx reticulatus* Davis and Dixon, a rather rare species, is a representative of the tubercular form. The coexistance of the two species in western Texas and northern Mexico is the only known situation where the two types occur sympatrically and makes an ideal comparative study possible. A study of *C. brevis* in sympatry with *C. reticulatus* should be useful in understanding interspecific relationships and in determining differences in life history strategies between the two types.

The primary objectives of this study are: 1) to describe certain life history phenomena of the two species, and 2) to document any geographic morphological variation that may be noted in *Coleonyx brevis*. Research on natural history is centered on describing the reproductive biology and food habits of *C. brevis* and the thermal ecology and general behavior of both species. Reproductive data are used to determine the breeding cycle and size at sexual maturity and to define the reproductive strategy of *C. brevis*. Data on food habits and feeding behavior are employed in revealing the feeding strategy of *C. brevis*. Temperature data are used in describing diurnal and nocturnal thermoregulatory habits and temperature preferences of both species. General behavioral data from each species are compared.

Ecological information is used to compare niche dimensions of each species and to describe some of the mechanics of niche separation, which enable the two to coexist. Geographic variation in morphology of *Coleonyx brevis* is analyzed and related to the taxonomic problem of speciation.

MATERIALS AND METHODS

Though Coleonyx brevis is a common species, C. reticulatus is known from less than 20 specimens; consequently, this thesis is weighted heavily with information on C. brevis. All of the data on live C. reticulatus are from two specimens kept in the laboratory. The ecologies of the two species are compared when justified.

Reproduction

A total of 201 specimens of C. brevis, collected from January to September of various years, was analyzed for reproductive data. In males, testes were measured (length and width) to the nearest 0.1 mm with the aid of an ocular micrometer in a dissecting microscope. From these data, testis volumes were calculated, using the formula for the volume of an ellipsoid: $V = 4/3\pi ab^2$, where a equals half the longest diameter and b equals half the shortest diameter at the widest part of the testis. The amount of convolution in vas deferens also was noted.

In females, ovarian follicles and oviductal eggs were counted and measured in situ; the diameters of follicles and the lengths and widths of eggs were recorded. All measurements were taken under a dissecting microscope and measured to the nearest 0.1 mm with the aid of an ocular micrometer. Eggs laid during the summer of 1973 by four females in captivity were measured with vernier calipers.

Thermal Ecology

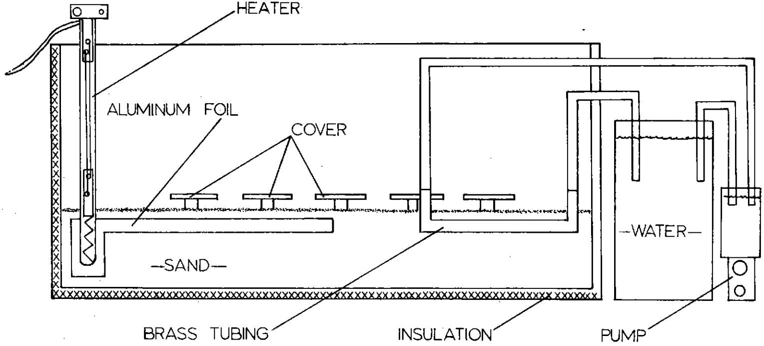
Temperature data were taken with respect to diurnal and nocturnal thermoregulatory habits and temperature preferences of *C. brevis* and *C. reticulatus*. All temperatures were taken with either a Schultheis fast reading cloacal thermometer or a Yellow Springs multichannel telethermometer. Temperature data were recorded on *C. brevis* collected in Brewster, Terrell, Val Verde, and Hidalgo counties, Texas, and Coahuila, Mexico, and on *C. reticulatus* collected in Brewster and Presidio counties, Texas. During daylight hours *C. brevis* were collected by turning rocks. Data were recorded on cloacal, air (5 mm above ground), substrate, and cover temperatures, and amount of activity. At night, specimens of *C. brevis* and *C. reticulatus* were collected while they were active on the desert floor and paved roads. Data were recorded on cloacal, air (5 mm above ground), and substrate temperatures, and amount of activity.

On one occasion, at sunrise, an adult *C. brevis* was followed to a burrow under a rock. The gecko was collected, a thermal probe inserted into its cloaca, and returned to the burrow. Three additional probes were used to register temperatures of the substrate under the rock, the rock surface above the burrow, and the air in the burrow.

To observe thermoregulatory behavior under cover in the laboratory, a rock was supported over a burrow, in sand substrate, in a terrarium. Brass tubing was buried 5 mm beneath the sand and ice water was passed through it. A 100 watt incandescent light bulb with reflector was directed to the top of the rock. Coleonyx brevis were introduced into the terrarium. A separate gecko was used for each of twelve tests. Geckos were allowed time to explore the terrarium and each took cover under the rock almost immediately. To allow for simulation of cooler (spring) and warmer (summer) conditions, nine tests were conducted in which substrate temperatures were less than 24°C and three tests in which substrate temperatures were more than 24°C. Within five minutes after geckos were under cover, data were recorded on cloacal, substrate, and bottom side of rock temperatures.

To define the temperature preferences of both species, a thermal gradient chamber was constructed in the laboratory (Fig. 1) (Dial, 1975). The chamber was a glass terrarium (92 x 27 x 27 cm) insulated on the floor, two sides, and one end with 1/4 in. styrofoam. Sixty mm of sand were used as a substrate. Heat was provided at one end by a 150 watt, thermostat equipped, aquarium heater. One end of a sheet of aluminum foil was wrapped around the heating element. The tip of the heater was buried in the sand, to the top of the heating element, at the insulated end of

Figure 1. A cutaway view of the laboratory thermal gradient.


HEATER
ALUMINUM FOIL
COVER
—WATER—
—SAND—
BRASS TUBING
INSULATION
PUMP

the terrarium. The remainder of the foil was doubled into a sheet 145 x 75 mm. The sheet was buried 5 mm below the surface of the sand and extended from the heater to approximately the center of the terrarium. Five masonite cover items (145 x 75 mm) on small wooden blocks were spaced 70 mm apart, the length of the terrarium. At the opposite end of the terrarium brass tubing (12 mm diameter) was used as a cooling element. The tubing was shaped into an "S" pattern and buried 5 mm below the surface of the sand. A seven liter aquarium was placed adjacent to the uninsulated end of the terrarium. An aquarium pump and filter (Dynaflo Motor Filter by Metaframe) was mounted on the aquarium and was used to circulate cold water from the aquarium, through the brass tubing, and back to the aquarium. The chamber produced a gradual thermal gradient from approximately 35 mm from the heating element to the cool end of the terrarium; the gradient ranged from 10° to 45°C. Lizards were introduced into the terrarium alternately at hot and cold ends. To allow lizards to be exposed to the full range of temperatures, recordings were taken only after lizards had occupied the chamber for one night (6-8 hours). Temperatures taken at the level of substrate at mid-body of resting geckos approximated cloacal temperatures and were considered as such.

Diet Composition

A total of 58 C. brevis and 3 C. reticulatus were examined for food. All *C. brevis* were collected in June and July, 1973, at Black Gap Wildlife Management Area, Brewster County, Texas. The *C. reticulatus* were collected in June and July, 1972 and 1973, in Brewster County, Texas.

Stomachs were removed from specimens and stomach volumes were determined to 0.1 cc by volume displacement using a graduated syringe. Numbers and volume of individual prey items were recorded for each stomach. Volumes of prey items were determined to 0.01 cc by volume displacement using a graduated insulin syringe. Prey items in each lizard stomach were counted individually.

Behavior

Behavioral data of *C. brevis* and *C. reticulatus* were recorded in the laboratory on the following aspects: exploratory behavior, walking, digging, climbing, aggregation, defensive behavior, territoriality, feeding, and interspecific interference. Three glass terraria (50 x 31 x 25 cm) were used as testing chambers. In each, 55 mm of sand were used as substrate. Cover items were pieces of clear plexiglass (18.5 x 8.8 cm) covered with a piece of black cardboard. Such an arrangement allowed for observance of lizards with minimal disturbance by lifting the cardboard. Red cellophane was taped over the walls and top of the terrarium. A 60 watt incandescent light bulb eight feet away allowed sufficient light for observation, but did not interfer with nocturnal activity.

Defensive behavior of both species was tested by presenting a predatory species of snake (Hypsiglena torquata texana) to geckos. Tests were conducted in the home terrarium of each gecko. Five tests were run on C. brevis using different geckos each time, and two tests were run on C. reticulatus using each gecko once.

Behavior on intraspecific territoriality in C. brevis was observed by presenting specimens of the same and different sexes to each other. For C. reticulatus, the two male specimens were enclosed together, alternately, in the home terrarium of each.

Feeding behavior of both species was observed during routine feeding sessions. To study the ability of C. brevis to innately perceive prey chemoreceptively, neonate unfed specimens were tested on chemical stimuli. The subjects, kept in a plastic beaker with moist paper toweling, were tested five days after hatching for responses to chemical stimuli. One hundred grams of crickets were placed in 20 ml hot distilled water (50°C) and stirred for 60 seconds. The liquid was poured off, centrifuged for 10 minutes at 2500 rpm, and the supernatant fluid was poured into small vials and refrigerated until used. Cotton swabs were used to present the extract to subjects. Distilled water was used as a control. During a test, a swab was brought to within 5 mm of the subject's mouth. If no positive reaction occurred within 30 seconds, a swab was brought into contact with the subject's mouth. Reactions (tongue flicks, attack) were recorded.

Adult C. brevis were tested for reactions to chemical stimuli in the following manner. Live mealworms were crushed in a glass petri dish. During a test, a cotton swab dipped in the body fluid was brought to within 10 mm of the subject's mouth. If no positive reaction occurred within 30 seconds, the swab was brought into contact with the subject's mouth. Reactions (tongue flicks, attack) were recorded.

Interspecific interference was observed by placing one speciman of each species in a neutral terrarium. Two cover items (masonite, 145 x 75 mm), one at each end of the terrarium, were available to the geckos. Observations on encounter reactions and choice of cover items were recorded.

Systematics

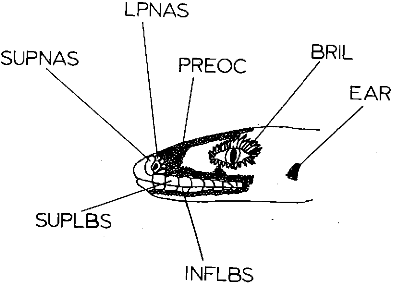
A total of 509 specimens of C. brevis and 16 specimens of C. reticulatus was examined for squamative data. All measurements were recorded in millimeters and were taken with vernier calipers, except snout-vent, left hind leg, and left fourth toe lengths, which were taken with a millimeter ruler. Measurements represent a straight line distance.

Snout-vent length (SVL), taken along the venter, was measured from the tip of the snout to the anterior border of the anal slit.

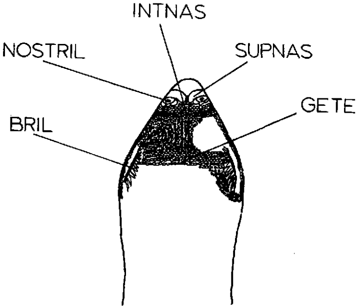
Left hind leg length (LHLL) was measured from the proximal area of the leg to the distal area of the fourth toe. Left fourth toe length (LFT) was taken from the base of the toe to the anterior edge of the toenail. Width of head at tympanum (WHAT) was taken at the center of the tympanum. Width of head at eye (WHAE) was taken at the center of the orbit. Head length (HEADL) was measured from the angle of the jaw to the tip of the snout.

Because of inconsistency in nomenclature of head scales, a drawing is included showing nomenclature used in this thesis (Fig. 2). Supranasals (SUPNAS) are scales between nostrils. Internasals (INTNAS) include all scales, other than supranasals, that border the nostril dorsally. Right and left postnasals (RPNAS and LPNAS) are all scales that border the nostril posteriorly, including the subnasal of Smith (1946). Supralabials and infralabials (SUPLBS and INFLBS) were counted to the anterior margin of the eye. All labial counts were taken on the right side of the head. Extrabrillar fringe scales (BRIL) were counted completely around the eye. Granules eye to eye (GETE) include all scales in a single row across the head between the centers of the orbits. Preoculars (PREOC) include all scales in a single row from the anterior margin of the eye to the posterior margin of the nostril. Preoculars were counted on the right side of the head. Fourth toe lamallae (FTL) were counted on the fourth toe of the left rear limb. Lamallae were counted from the base to the tip of the toe.

Figure 2. Typical scutellation of Coleonyx brevis. Abbreviations are defined on p. 13. (A) Lateral view of head. (B) Dorsal view of head.


LPNAS
SUPNAS
PREOC
BRIL
EAR
SUPLBS
INFLBS

A.


INTNAS
NOSTRIL
SUPNAS
GETE
BRIL

B.

Longitudinal scale rows around body (SAB) were counted at mid-body.

Sex was determined by examining the size of the cloacal spurs, development of preanal pores, and amount of swelling at the base of the tail. If original tails were present, the number of tail bands was counted. Regenerated tails were noted.

In C. reticulatus data were recorded on three additional characters: 1) number of dorsal scale rows from first to last row of tubercles (DSRS), 2) number of ventral scale rows from first to last row of tubercles (VSRS), and 3) number of longitudinal rows of tubercles (TUBROW).

Specimens of C. brevis were examined from 173 localities; specimens of C. reticulatus were examined from 15 localities. Because of the paucity of material from certain localities of C. brevis, it was often necessary to pool data from nearby localities. All localities and significant physiographic boundaries (e.g. mountains, unsuitable vegetation) were mapped before localities were pooled. Therefore, it was possible to determine if gene exchange could potentially occur between adjacent localities.

Computations were done on an IBM 360/65 computer using the Statistical Analysis System (SAS). Initial statistical analysis involved computation of standard statistics (range, mean, standard deviation, standard error of mean, and coefficient of variation) for 21 variables of all specimens. Next, all characters were submitted to a multivariate analysis of variance (MANOVA) using the SAS system. The 0.01 significance level was used for all tests.

Specimens from the following institutions and private collections were examined:

BBNP	Big Bend National Park Collection, Big Bend National Park, Texas
BCB	Bryce C. Brown Collection, Waco, Texas
BED	Ben E. Dial Collection, Dallas, Texas
DMNH	Dallas Museum Natural History, Dallas, Texas
FSH	Fred S. Hendricks Collection, College Station, Texas
FWMSH	Ft. Worth Museum of Science and History, Ft. Worth, Texas
KU	Museum Natural History, University of Kansas, Lawrence
LACM	Los Angeles County Museum, Los Angeles, California
RGW	Robert G. Webb Collection, El Paso, Texas
SM	Strecker Museum, Baylor University, Waco, Texas
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University, College Station
TNHC	Texas Natural History Collection, University of Texas, Austin
UIMNH	Museum Natural History, University of Illinois, Urbana
UMMZ	Museum Zoology, University of Michigan, Ann Arbor
UNM	Museum Southwestern Biology, University of New Mexico, Albuquerque

HISTORICAL SYNOPSIS

The genus belongs to the distributionally disjunct gekkonid subfamily Eublepharinae and is the only representative in the Western Hemisphere. What is known today as *Coleonyx brevis* was originally described as *Stenodactylus variegatus* (Baird, 1859). Boulenger (1885) suggested the name *Eublepharis variegatus* for specimens from Texas. Stejneger (1893) applied the name *Coleonyx variegatus* to the Sonoran Desert populations (California, Arizona, Nevada, and northwestern Mexico) and assigned the name *Coleonyx brevis* to representatives in the Chihuahuan Desert (Texas, New Mexico, and northeastern Mexico). Klauber (1945) considered the possibility of intergradation with *C. variegatus* but recognized *C. brevis* as a separate species. Subsequent students (Schmidt, 1953; Stebbins, 1954; Conant, 1958; Axtell, 1959; Minton, 1959) have been inconsistant in recognizing *C. brevis* as a distinct species. Smith (1933) described significant differences between the two species in number of preanal pores and shape of cloacal spurs. In his revision of the genus, Klauber (1945) presented data showing distinct morphological variation in *C. brevis* and *C. variegatus* by analyzing eight scale characters of each species. Correlation of some of his data with geographic areas indicated the need for a study on morphological variation in *C. brevis*. Smith (1946) described the size, color, and scalation of *C. brevis* and presented a key to all North American taxa within the genus. Kluge (1962) studied the osteology of most species within the genus. Dixon (1970) catalogued all that was known of _C. brevis_ and _C. variegatus_ up to that time.

Detailed studies on the reproductive ecology of lizards, particularly the family Iguanidae, have been conducted. However, most of the information on other families is in the form of miscellaneous notes. Such is the case for the subfamily Eublepharinae (Klauber, 1945; Anderson, 1963; Minton, 1966; Werner, 1972). Parker (1972) treated the reproductive biology of _C. variegatus_ with some detail. Other information on reproduction in this genus consists of notes on eggs and clutch size (Mulaik, 1935; Smith, 1946; Werler, 1951, 1970; Alverez del Toro, 1960; Davis and Dixon, 1961; Duellman, 1965; Shaw, 1967). Seasonal variation in reproductive cycles has been documented for many species of lizards (Mayhew, 1963, 1966; Fitch and Greene, 1965; Zweifel and Lowe, 1966; Greene, 1969a; Ballinger, Tyler, and Tinkle, 1972; Schrank and Ballinger, 1973; Parker and Pianka, 1973).

The initial study on thermal ecology in reptiles (Cowles and Bogert, 1944) has served as a reference for subsequent authors. There is an ample amount of literature on the thermal ecology of temperate, diurnal species (Fitch, 1956; Mayhew, 1963; Soule, 1963) and tropical, diurnal species (Inger, 1959; Ruibal, 1961; Lee and Badham, 1963) but relatively few studies have been conducted on nocturnal species. Bustard (1967) studied thermoregulation and activity cycles of Gehyra variegata and Bustard (1968) discussed thermal dependent activity in Diplodactylus vittatus. Several species of geckos were studied by Licht et al., (1966). Vance (1973) demonstrated laboratory temperature preferences and Parker and Pianka (1974) included notes on field temperatures of C. variegatus.

Many publications on food habits of lizards are available. However, as in other areas of natural history, eublepharine geckos have been neglected. Smith (1946) listed a few food preferences of C. variegatus. Parker and Pianka (1974) gave qualitative and quantitative data on food of C. variegatus and Punzo (1974) analyzed stomach contents of C. brevis from Big Bend National Park, Texas.

Ecological studies contrasting niches of closely related species are common in the literature. Differences in food type and size have been examined for many groups of organisms (birds, by Schoener, 1965; insects, by Hutchinson, 1959; amphibians, by Jaeger, 1972). Partitioning of space has been well documented in the lizard genus Anolis (Schoener, 1968) and in numerous other tropical lizard species (Rand and Humphrey, 1968). Pianka (1969) examined ecological differences in "place," "food," and "time" niches of sympatric species of Ctenotus.

Ethological studies of reptiles have become more common in recent years. Lizards, especially iguanids with their elaborate territorial and breeding displays, have received much attention (Carpenter, 1961, 1962, 1966). Studies on predatory behavior have emphasized the importance of sensory abilities of reptiles (Burghardt, 1970; Burghardt and Abeshaheen, 1971). These studies revealed the magnitude chemical stimuli play in predatory behavior. The importance of visual stimuli has been demonstrated by Herzog and Burghardt (1974). Gamow and Harris (1973) have shown that thermoreception abilities play an important role in predatory behavior of snakes.

The interrelation of olfactory structure and function in the feeding behavior of reptiles was studied by Stebbins (1948). He has shown that large conchae in the nasal chamber, in conjunction with extensive areas of olfactory epithelium, suggest a well-developed olfactory function in lizards. Noble and Kumpf (1936) stated that odorous particles are conveyed to the Jacobson's organ via the tip of the tongue. Bellairs (1949) demonstrated that a long tongue and well-developed Jacobson's organ in the genus Varanus is indicative of a strong vomernasal sense in the behavior of the lizards.

The mechanics of feeding behavior was reviewed by Bellairs (1970). His treatise, relating cranial structure to feeding function, touched on most lizard groups.

Social and breeding behavior of C. variegatus were elaborately outlined by Greenburg (1943). Activity patterns were noted by Brattstrom (1952) and Evans (1967) and Bustard (1963) discussed tongue wiping in *Coleonyx*. Miscellaneous publications (Cope, 1880; Smith, 1946) have noted several aspects of behavior of eublepharines.

Very little information is available on *C. reticulatus*. From 1958 to 1972 only the type specimen was known. Kluge (1962) examined X-rays of the type specimen. Dixon's (1970) account summarized all that was known of the species to that time. Since 1972 less than 20 specimens have been recorded. Seifert and Murphy (1972) reported on additional specimens and included notes on scalation, coloration, clutch size, and habitat. Seifert et al., (1973) reported on range extensions for the species. Included in their account were notes on egg size and parasites. Hendricks (1973) reported on additional specimens and Robert G. Webb (pers. comm.) recorded one specimen from Durango, Mexico.

THE LIZARDS

Coleonyx brevis is a small, terrestrial gecko with a maximum snout-vent length of 63 mm. *Coleonyx reticulatus* is a larger gecko with a maximum snout-vent length of 94 mm. Both species are similar in body proportions and physique. Comparative weights and snout-vent lengths are listed in Table 1.

Coleonyx brevis (Fig. 3) belongs to the group of small, non-tubercled geckos of the southwestern United States and Mexico. Juveniles are creamy yellow with four brown, even-edged cross-bands on the dorsum (between the limbs) and one crossband on the neck. The tail has 6 to 11 narrow brown bands. The dorsal cross-bands of subadults become irregularly edged on a lighter yellow-buff background. The crossbands fade towards maturity and many old adults become mottled with brown spots. The venter of juveniles and adults is cream colored with no markings. Limbs are spotted with dark brown and tan.

Coleonyx reticulatus (Fig. 4) belongs to the group of large, tubercled geckos of Texas, Mexico, and Central America. Adults are pink-buff in coloration. The head and dorsun are covered with a profusion of small to medium auburn spots. Frequently, spots converge to form reticulations with irregular borders. Limbs are covered with small auburn spots. The tail has a series of irregular broken bands. The gular region, venter, and ventral part of

Table 1. Representative weights and respective snout-vent lengths of adult *Coleonyx brevis* and *Coleonyx reticulatus*. Snout-vent lengths are in mm, weights are in grams.

Coleonyx brevis					*Coleonyx reticulatus*				
Specimen	Number	Sex	SVL	Weight	Specimen	Number	Sex	SVL	Weight
BED	307	M	51	2.0	BED	292	M	86	9.8
BED	314	M	51	2.0	BED	348	M	76	6.8
BED	306	F	53	2.1					
BED	305	F	54	2.5					

Figure 3. Lateral view of adult Coleonyx brevis, female, from Black Gap Wildlife Management Area, Brewster County, Texas. (snout-vent length, 54 mm)

Figure 4. Lateral view of adult Coleonyx reticulatus, male, TCWC No. 48208, from Black Gap Wildlife Management Area, Brewster County, Texas. (snout-vent length, 86 mm)

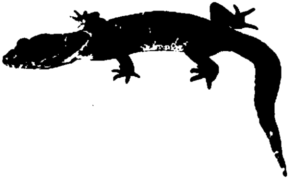


FIGURE 3

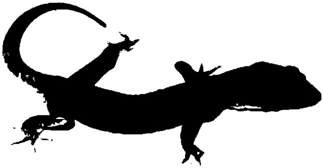


FIGURE 4

the tail are pinkish in coloration. The abdominal skin is somewhat transparent.

RANGE AND HABITAT

Coleonyx brevis is distributed from southeastern New Mexico, Trans-Pecos Texas, and southwestern Texas, south into eastern Chihuahua, northeastern Durango, Coahuila, northern Nuevo Leon, and northern Tamaulipas, Mexico (Fig. 5). The range of C. brevis lies within the Chihuahuan, Balconian, and Tamaulipan Biotic Provinces in Texas (Blair, 1950) and the Chihuahuan-Zacatecas and Tamaulipan Biotic Provinces in Mexico (Goldman and Moore, 1946).

Coleonyx reticulatus appears to be completely sympatric with C. brevis, for it is known only from Brewster and Presidio counties, Texas (Davis and Dixon, 1958; Seifert et al., 1973; Hendricks, 1973) and one locality (7 miles southwest of Leon Guzman) in Durango, Mexico (Robert G. Webb, pers. comm.) (Fig. 6). Coleonyx reticulatus occurs within the Chihuahuan Biotic Province in Texas (Blair, 1950) and the Chihuahuan-Zacatecas Biotic Province in Mexico (Goldman and Moore, 1946).

The Chihuahuan Desert is composed of xeric plains interrupted irregularly by islands of mountains. Mountains usually extend north to south and dissect the plains into a mosaic of flatlands connected by passages. The mountains consist of domes of Upper Cretaceous limestone separated by areas of Upper Cretaceous marls, chalks, and sandstones (Baker, 1956). The highest summits occur in the Sierra Madre Oriental, Sierra del Carmen, Chisos, Davis,

Figure 5. Geographic distribution of _Coleonyx brevis_. An "X" marks the study area.

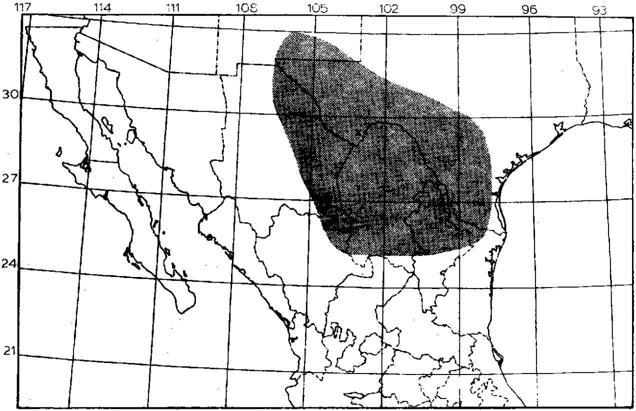
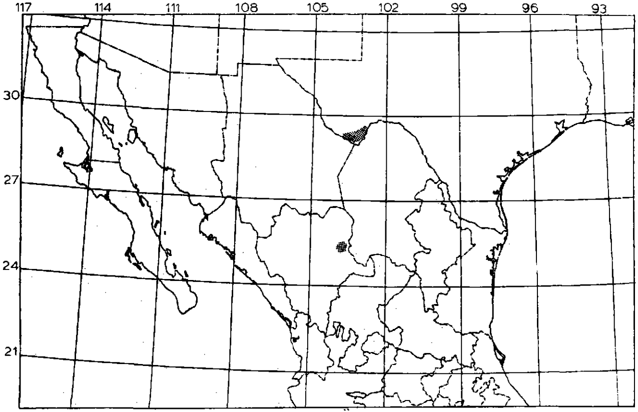

117
114
111
108
105
102
99
96
93
30
27
24
21

Figure 6. Geographic distribution of Coleonyx reticulatus.



117
114
111
108
105
102
99
96
93
30
27
24
21

and Guadelupe Mountains and are composed of volcanic rocks. The desert plains are marked by scattered buttes, low hills with massive rimrock, and igneous knobs (Baker, 1956). Baker (1956) refers to the desert areas lying west of the Sierra Madre Oriental as the Mesa del Norte.

All of the Chihuahuan Desert is arid with most thunderstorms occurring in the summer months. During the summer rains, arroyos fill and empty into rivers leaving small, isolated pools of standing water. Higher altitudes receive more rainfall and have less evaporation. Hence, they support more luxuriant vegetation; oak and pine forests are found in the highest elevations. Muller (1947) attributes the aridity of the Chihuahuan Desert to its latitudinal position within the subtropical high-pressure belt. Most of the southern parts (Mesa del Norte) of the desert occur in the wind shadow of the Sierra Madre Oriental. To the north the desert lies too far inland to receive the moisture-laden air from the Gulf of Mexico.

The semi-arid brushlands of southern Texas and eastern Coahuila (the "Gulf Coastal Plain" of Baker, 1956) have little topographic relief. Most of the area is composed of Upper Cretaceous rocks overlain with gravels and aeolian deposits (Baker, 1956). Rainfall is moderate; the eastern slopes of the Sierra Madre Oriental receive considerably more moisture than do the western slopes. The Gulf Coastal Plains receive moisture from the

Gulf of Mexico for several months of the year.

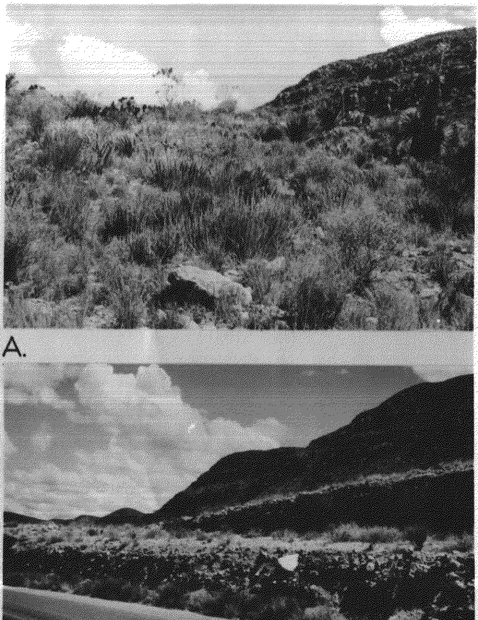
Plants characteristic of the Chihuahuan Desert include: Sotol (Dasylirion leiophyllum), Yucca (Yucca rostrata), Creosote (Larrea divaricata), Ocotillo (Fouqueria splendens), Lechuguilla (Agave lecheguilla), Candelilla (Euphorbia antisyphilitica), and Chino Grama (Bouteloua breviseta).

Coleonyx brevis habitat is characteristically xeric and semi-xeric areas of the Chihuahuan Desert and brushlands of southern New Mexico, western and southern Texas, and northern Mexico. Within this area the species occurs from approximately 300 to 1500 meters above sea level. Specimens are found most commonly in arid flatlands or plains, or at the bases of mesas and buttes. The species is usually restricted to parts of the area where gravely or rocky, well-drained soils occur. During daylight hours in the spring, specimens can be found under rocks, fallen yuccas, and other cover items. In the extreme heat of summer, geckos move further into the earth and can be found under larger rocks and in crevices between rocks.

Coleonyx reticulatus is found in xeric areas of the Chihuahuan Desert. The species has been collected only in very rocky areas with some topographic relief. The type specimen is from a hillside cluttered with volcanic rocks. One specimen was found in an abandoned cinnabar mine. All other specimens were collected at night on roads between or near highway cuts through rocky hillsides.

All specimens collected on roads were active during or after summer thunderstorms. Figure 7 illustrates the typical habitat of *C. brevis* and *C. reticulatus*.

Figure 7. Habitat of _Coleonyx_ _brevis_ and _C._ _reticulatus_. (A) Typical Chihuahuan Desert with _Yucca_ _rostrata_, _Euphorbia_ _antisyphilitica_, _Agave_ _lecheguilla_, and _Bouteloua_ _breviseta_. Both species of _Coleonyx_ were collected in this habitat. (B) Both specimens of _C._ _reticulatus_ were collected within 15 meters of this road cut. This photo was taken 8 meters east of (A).


A.
B.

ECOLOGY AND ETHOLOGY

Reproduction

Reproductive cycles of lizards have received considerable attention in recent years and two basic patterns exist. In tropical areas with relatively little seasonal temperature change, and with food and moisture readily available, most species are characterized by a year-round breeding pattern (Church, 1962; Wilhoft, 1963). Because of seasonal variation in temperature and food, most temperate species exhibit a different pattern. Generally, in the spring temperate lizards emerge from hibernation in, or rapidly reaching, a reproductive condition, with enlarged testes in males and mature ova in females. Lizards mate shortly thereafter, ovulation follows, and in the case of oviparous forms, egg laying takes place during late spring and early summer. Eggs hatch during summer and by early fall testes have decreased to minimum size and ovarian follicles have atrophied. Such cycles are the result of stimulation of the endocrine system by a variety of environmental stimuli (photoperiod, temperature, moisture).

Species native to southern temperate areas tend to reproduce over a greater part of the year than do species from more northern areas (Cagle, 1950; Hamlet, 1952; Burkett, 1962). In wide ranging species, females in southern populations generally produce more egg clutches per breeding season than do females in northern populations (Fitch and Greene, 1965; Pianka, 1970a).

The only information available on reproduction in Coleonyx reticulatus is on clutch size (2 eggs) (Seifert and Murphy, 1972) and on oviposition date (13 July 1971) and egg size (24 x 17 mm, 32 x 18 mm) (Seifert et al., 1973). The following account is an analysis of the reproductive ecology of C. brevis.

Reproductive Cycles of Males

As is typical of most temperate lizards, testis size of C. brevis varies considerably during the year. In other species, enlarged testes have been shown to indicate sexual maturity (Tinkle, 1961; Parker and Pianka, 1973). To determine size at sexual maturity, all males of C. brevis that were collected during the breeding season were examined. When testis volume is compared to snout-vent length, it is observed that enlargement of testes occurs in specimens 45 mm and larger (Fig. 8) and sexual maturity in males apparently occurs at that size. In each male examined the left testis lay anterior to the right testis.

A comparison of the ratio testis volume/snout-vent length to the collection date (Fig. 9) reveals that considerable testis enlargement occurs in the spring and early summer; Figure 10 summarizes the variation that occurs in average testis volume during the year. When lizards emerge from hibernation, testes are medium in size. During April and May testes rapidly increase in volume

Figure 8. Scatter diagram showing the relation between snout-vent lengths and testis volumes of male *Coleonyx brevis*. Measurements are from specimens collected during breeding seasons only.

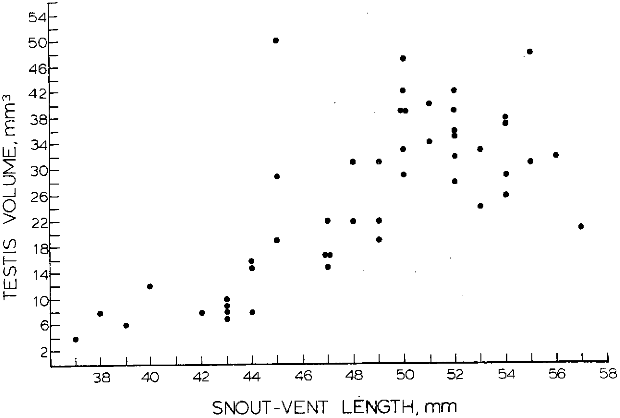
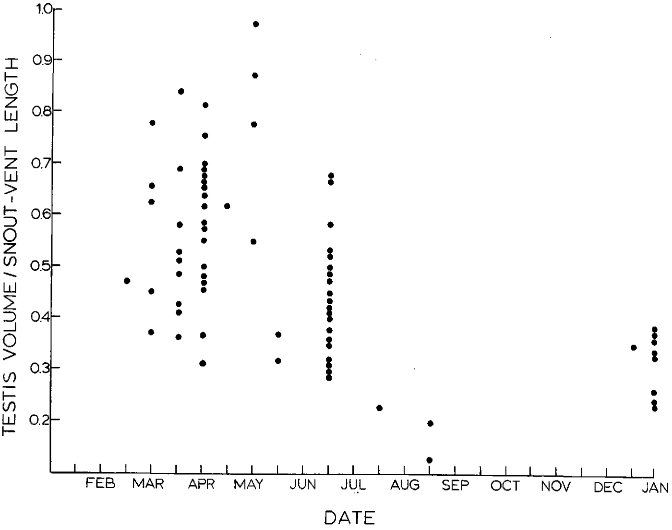
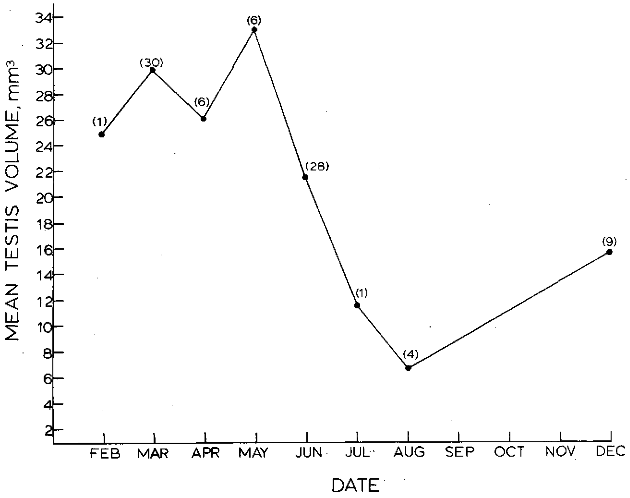

TESTIS VOLUME, mm^3
54
50
46
42
38
34
30
26
22
18
14
10
6
2
38
40
42
44
46
48
50
52
54
56
58
SNOUT-VENT LENGTH, mm

Figure 9. Scatter diagram showing the relation between the ratio testis volume/snout-vent length and the collection date of adult male <u>Coleonyx</u> <u>brevis</u> (> 44 mm).



TESTIS VOLUME / SNOUT-VENT LENGTH
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
DATE

Figure 10. Monthly changes in testis volume means of potentially breeding male *Coleonyx brevis* (> 44 mm). Numbers in parentheses represent sample sizes.


MEAN TESTIS VOLUME, mm³
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
DATE
(1)
(30)
(6)
(6)
(28)
(1)
(4)
(9)

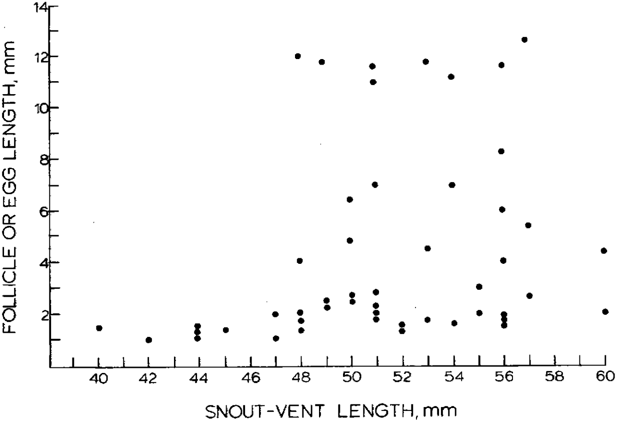
until maximum size is attained, and from June to August testes reduce in size. No males were collected in September, October, or November; however, testis size in those months is probably minimal. Testes begin to enlarge in December, January, and February, and approach reproductive size when the lizards emerge from hibernation.

Of special interest is the rapid decrease in testis volume during June, July, and August; however, by examining Figure 9, p. 43, one can observe that males are reproductive as late as mid-June. This pattern is similar to the closely related species, Coleonyx variegatus (Parker, 1972) and to temperate species of other families (Woodbury and Woodbury, 1945; Schrank and Ballinger, 1973).

Reproductive Cycles of Females

To determine size at sexual maturity in females, all specimens collected during the breeding season were autopsied. When follicle and egg size is compared to snout-vent length (Fig. 11), it is observed that enlargement of eggs occurs in specimens 48 mm and larger; specimens in this size group are considered adults. In all specimens, the left ovary lay anterior to the right. In females with developing follicles, one follicle in each ovary was always more developed than the others, and two eggs (one per oviduct) were found in all egg-bearing females. Frequently, one egg was considerably larger than the other; however, this occurred

Figure 11. Scatter diagram showing the relation between snout-vent lengths and follicle and egg sizes of female *Coleonyx brevis*. Measurements are from specimens collected during breeding seasons only.


14
12
10
8
6
4
2
FOLLICLE OR EGG LENGTH, mm
40
42
44
46
48
50
52
54
56
58
60
SNOUT-VENT LENGTH, mm

in each oviduct in approximately equal frequency.

By comparing follicle and egg size of potentially breeding females to date of collection (Fig. 12) the reproductive cycle of females can be predicted. Females emerge from hibernation with very small, unyolked follicles, ovarian follicles enlarge soon after, yolk deposition occurs, and ovulation follows. First mating probably occurs in early April (one specimen, collected 10 April, contained oviductal eggs 6.0 x 4.7 mm). Oviductal eggs increase in length throughout the spring (range = 4.0 to 12.6 mm) and length at oviposition averages 12.00 mm. Large eggs were found in females through mid-August; thus, egg laying occurs from late spring to late summer.

Many adult females collected in mid-summer had small yolked follicles, no ovarian eggs, and no corpora lutea. Perhaps such specimens had recently deposited eggs, as corpora lutea probably disappear shortly after eggs are laid. Figure 13 summarizes the sequence of events in male and female reproductive cycles.

Sexual Dimorphism

Females average slightly larger than males (Fig. 14) and may be easily distinguished from males by the lack of well-developed cloacal spurs at the base of the tail. In males, the spurs are curved forward and upward. In addition, males possess well-developed preanal pores anterior to the anal slit; females possess

Figure 12. Scatter diagram showing the relation between follicle and egg size and collection date of adult female Coleonyx brevis (> 48 mm).

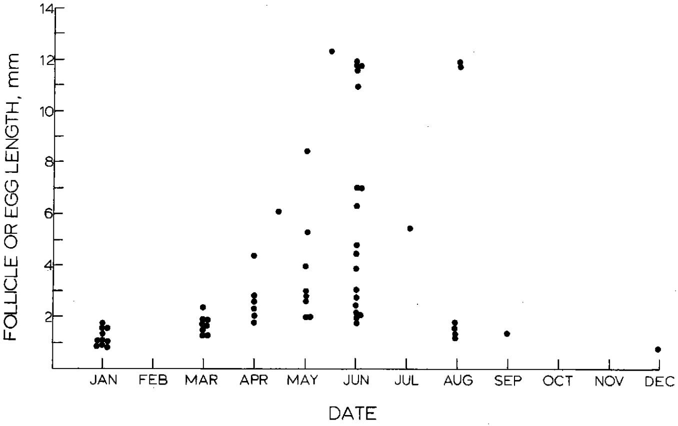

FOLLICLE OR EGG LENGTH, mm
14
12
10
8
6
4
2
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
DATE

Figure 13. Seasonal occurrence of reproductive conditions of adult male (> 44 mm) and female (> 48 mm) *Coleonyx brevis*.

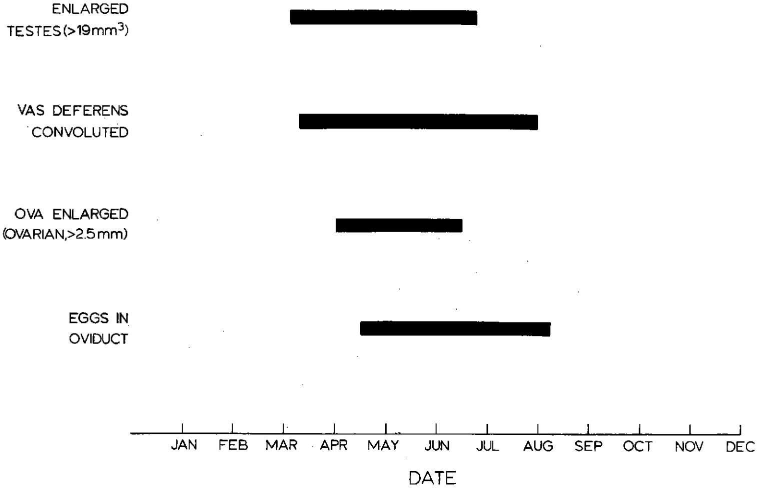
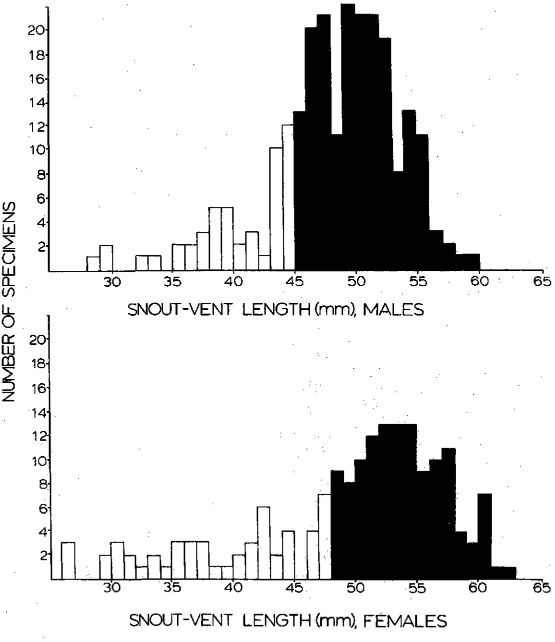

ENLARGED TESTES (>19mm³)
VAS DEFERENS CONVOLUTED
OVA ENLARGED (OVARIAN,>2.5mm)
EGGS IN OVIDUCT
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
DATE

Figure 14. Histograms showing sexual dimorphism in snout-vent lengths of male and female *Coleonyx brevis*. Shading indicates sexually mature specimens.


NUMBER OF SPECIMENS
20
18
16
14
12
10
8
6
4
2
30
35
40
45
50
55
60
65
SNOUT-VENT LENGTH (mm), MALES
20
18
16
14
12
10
8
6
4
2
30
35
40
45
50
55
60
65
SNOUT-VENT LENGTH (mm), FEMALES

poorly developed (non-glandular) preanal pores.

Eggs and Young

During the summer of 1973 four captive females laid eggs that were soft, leathery, and adherent (Fig. 15) and data on the adults, eggs, and young are presented in Tables 2 and 3. Eggs were kept partially buried in moist vermiculite in glass jars and incubated at relatively low temperatures (20-24°C). Consequently, a long incubation time was necessary for eggs to reach maturity. Bellairs (1969) noted that as little as one degree centigrade in incubation temperature may result in a four to five day difference in incubation time. Natural environmental temperatures in west Texas are much warmer than laboratory temperatures and therefore, in natural conditions, incubation time would have been shorter.

Eggs one and two were kept relatively dry for the first two weeks and each showed signs of desiccation. When substrate moisture content was increased, the eggs regained the original turgid form. It is likely that females lay their eggs in microhabitats that contain considerable moisture if eggs are to develop successfully.

Reproductive Strategies

Differences in approaches to life history patterns and reproductive strategies have been analyzed by several authors (Cole,

Figure 15. One clutch of eggs of Coleonyx brevis, laid and photographed 24 June 1973. Top egg measured 6.6 x 12.5 mm, bottom egg measured 6.7 x 13.6 mm. Eggs were leathery and adherent.

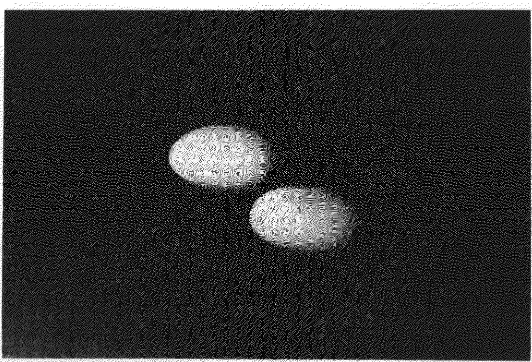


FIGURE 15

Table 2. Data on gravid adult, egg size and development, and hatching date of *Coleonyx brevis*. Snout-vent lengths of adults are in small parentheses. Egg sizes are length x width, mm.
* indicates date of oviposition.

Date	Egg 1	Egg 2	Egg 3	Egg 4	Egg 5	Egg 6	Egg 7	Egg 8
24 June *	12.5x6.6 (51)	13.6x6.7 (51)	11.7x6.7 (52)	11.7x6.9 (52)				
2 July	13.0x6.8	13.9x6.8	12.3x7.1	12.1x7.8	12.0x5.5 8 July *	11.7x6.6 8 July *		
19 July	13.1x7.8	14.5x7.5	Atrophied	12.4x8.3	12.1x7.1	12.0x7.1	11.4x6.2 16 July *	11.2x6.3 16 July *
28 July	13.6x8.5	14.4x8.3	---	13.0x8.7	12.2x7.6	12.0x7.5	11.5x7.3	11.3x7.3
5 August	13.8x8.7	14.4x8.4	---	13.3x8.9	12.2x7.6	12.1x7.9	11.3x7.0	11.2x7.4
13 August	14.7x9.2	14.8x9.1	---	14.2x9.1	12.7x8.1	12.9x8.4	11.7 (length)	11.4 (length) (adhered)
19 August	15.0x9.3	15.3x8.9	---	14.8x9.4	12.9x8.5	12.3x8.8	11.8x8.2	11.7x8.5 (separated)
26 August	15.5x9.6	15.9x9.5	---	15.2x9.6	13.1x8.6	12.7x8.9	12.1x8.5	11.9x8.7
5 September	16.7x10.0	16.8x10.0	---	16.5x9.8	13.9x9.2	13.1x9.1	12.9x8.9	12.8x9.1
1 October	Atrophied	Opened, well-developed	---	Atrophied	Hatched	13.1x8.1	---	---
2 October	---	---	---	---	---	Atrophied	13.1x8.3	12.9x8.3
4 October	---	---	---	---	---	---	Hatched	---
5 October	---	---	---	---	---	---	---	Hatched

Table 3. Data on egg size, egg weight, hatching date, hatchling size, and hatchling weight of *Coleonyx brevis*. Sizes are in mm, weights are in grams.

Egg No.	Egg Size At Hatching	Egg Weight At Hatching	Hatching Date	Hatchling Size	Hatchling Weight
5	---	---	1 October	24	0.24
7	13.1x8.3	0.49	4 October	26	0.26
8	12.9x8.3	0.49	5 October	25	0.21

1954; Lack, 1954; Williams, 1966). Generally speaking, each is a result of environmental conditions effecting selection to produce the strategy most profitable for a species in a particular environment. Basically, there are two reproductive strategies, each related to stable and non-stable climatic conditions. Some species, characteristic of regions with variable climates, are early maturing, short lived, and have a high annual reproductive effort. Other species, characteristic of rather stable environments, live for several years and have a low annual reproductive effort. Selection favoring such strategies has been termed, respectively, "r" selection, r referring to the intrinsic rate of increase, and "K" selection, K referring to the carrying capacity of a particular environment (MacArthur and Wilson, 1967). No species are completely r-selected or K-selected; however, most show definite trends to one of the two and can be categorized as such (Pianka, 1970b).

In a K-selected environment, population density approaches the carrying capacity of the environment, competition is strong, and emphasis is placed on increased individual efficiency. Annual reproductive effort is minimal, with emphasis placed on maximum fitness of young. In an r-selected environment, population density is low and competition is reduced. Reproductive energies are aimed at rapid reproduction with a minimal amount of energy allocated to individuals.

Information available on lizard life histories suggests that selection works in reverse to that predicted by MacArthur and Wilson (1967) and Pianka (1970b). Tinkle (1969) and Tinkle et al., (1970) discussed the evolution of lizard life histories and Tinkle (1969) made the following predictions regarding lizard life history patterns. First, lizards that live in areas with long periods favorable to reproduction will (1) lay multiple clutches per season, (2) have short life spans, (3) reach sexual maturity early, and (4) have maximum risks during reproductive activity. Second, lizards that live in areas with short reproductive seasons will (1) lay single clutches per season, (2) be long lived, (3) have delayed sexual maturity, and (4) have minimum risks during reproductive activity. Data on Coleonyx brevis suggest that the species is intermediate with respect to Tinkle's predictions; each prediction with regards to C. brevis is discussed below.

Number of clutches per year. The length of eggs laid in the summer of 1973 averaged 12.00 mm; eggs 10 to 12 mm in females collected in May and June (Fig. 12, p. 51) were probably ready to be laid. Incubation time in C. variegatus is six weeks (Parker, 1972); Werler (1970) reported that C. brevis hatched in 30 days. Allowing four to five weeks for incubation time, the first young C. brevis of the year would appear in mid-June. Data from museum specimens examined support this: hatchlings (27 mm) were collected 14 June and 24 June. Parker (1972) suggested a four week period between successive clutches of eggs in C. variegatus, which is probably accurate for C. brevis as well. Female C. brevis laying eggs in mid or late May could lay again in late June or late July. If incubation time is four to five weeks, hatchlings would appear in late June, late July, and late August and data from museum specimens support this: hatchlings were collected 15 July (30 mm), 25 July (30 mm), 11 August (30 mm), 12 August (27 mm), 22 August (28 mm), and 27 August (29 mm). It is concluded that female C. brevis produce two clutches per reproductive season. Though not as many clutches as in some of the more r-selected species, C. brevis represents a multiple clutched species.

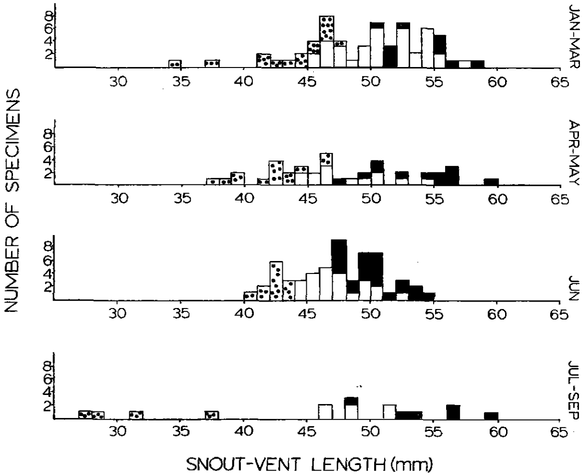
Several multiple clutched species reproduce well into late summer and early fall (Fitch, 1970) and such a strategy is an attempt to get as much out of a reproductive season as possible. Data reveal that hatchlings of C. brevis were collected throughout late spring and summer. Though they could be the young of first year adults reaching sexual maturity and reproducing at successive dates throughout the summer, some are doubtlessly the result of multiple clutches in second year adults. Tinkle (1969) stated that in a cyclic environment there will be some point in the season at which another reproduction, while possible, will contribute very little to the fitness of the female. A female that refrains from producing the last possible clutch may increase her fitness by increasing her chances for successful reproduction the following spring, compared to a female that does lay another clutch. Tinkle (1969) suggested that females might use the now longer non-reproductive season for growth.

A variation of this may occur in C. brevis. Fat storage in tails has been documented in several species (Zweifel and Lowe, 1966; Greene, 1969b)and occurs in C. brevis. Greene (1969b) suggested that the amount of fat body deposition may be inversely related to ovarian cycles. Steatocaudic species utilize fat stored in the tail to supply energy for winter hibernation and spring gonad development (Hahn and Tinkle, 1965). As discussed in another section, C. brevis frequently autotomize the tail to escape predation. Autotomy probably occurs most often during the breeding season when individuals are most active and, consequently, individuals enter late summer and fall with newly regenerated tails. Foregoing egg production in late summer and early fall may aid in development of a newly regenerated tail. The longer non-reproductive season at the end of the summer may be used for tail development, to insure successful hibernation and gonad development, and ultimately to increase fitness.

Life expectancy. Little regarding turnover can be determined from available data; however, Moehn (1962) reported a longevity record of 14 years for a captive C. variegatus. Surely, because of intrinsic and extrinsic factors effecting natural populations, individuals in nature have shorter life spans. Coleonyx brevis probably have low annual turnover when compared to species with high annual mortality (Sceloporus olivaceus, Blair, 1960; Callisaurus draconoides, Pianka and Parker, 1972). Adult C. brevis represent more than half of the lizards in spring and summer samples (Fig. 16). Based on Moehn's record, members of the genus can be assumed to be relatively long lived species.

Age at sexual maturity. Size distribution of immature and adult specimens is illustrated in Figure 16; "January-March" represents the period when lizards are emerging from hibernation, "April-May" and "June" when lizards are most reproductively active, and "July-September" the close of the reproductive season. The small number of immature geckos present throughout the breeding season (April-June) suggests that geckos reach sexual maturity at the end of their first year. Geckos that are 42 mm in April probably reach sexual maturity by the following summer, but individuals that are 42 mm in June probably are not capable of reproduction that summer. More than likely, such specimens represent hatchlings from late August and September of the previous year. However, geckos that hatch early in one season could quite possibly reproduce the following season; individuals that are 41-42 mm in "January-March" and 43-44 mm in "April-May" (Fig.16) represent such lizards. The data suggest that C. brevis mature in approximately twelve months and may be considered a relatively early maturing species.

Figure 16. Histograms showing seasonal snout-vent length distribution and seasonal variation of age and sex groups of Coleonyx brevis. Dotting indicates juveniles, open indicates males, shaded indicates females.


NUMBER OF SPECIMENS
JAN-MAR
APR-MAY
JUN
JUL-SEP
2
4
6
8
30
35
40
45
50
55
60
65
SNOUT-VENT LENGTH (mm)

Risks. Tinkle (1969) has outlined certain risks involved during reproduction in early maturing species. Short lived, early maturing species have relatively shorter time in which to produce a certain number of young. Therefore, to insure successful mating, such forms tend to take more risks during the breeding season than do late maturing, long lived species. Long lived species have multiple seasons in which to reproduce and hence are able to take fewer risks. Ultimately, risks aid in maintaining an adequate annual reproductive effort.

Tinkle (1969) used the following risks to compare early and late maturing species: weight per clutch in relation to body weight, conspicuous sexual coloration, elaborate courtship, aggressiveness, and multiple clutches. Tinkle (1969) stated that multiple clutches are frequently characteristic of long lived species and his data reveal that risks taken by short lived species may be twice as high as in long lived species. No data are available for C. brevis on weight per clutch in relation to body weight, but of the remaining four risks, one (multiple clutches) is characteristic of C. brevis.

The strategy. From the reproductive characteristics discussed above, the reproductive strategy of C. brevis can be defined. Two characteristics of C. brevis, multiple clutches and age at sexual maturity, are characteristic of r-selected forms, while two characteristics are definitely K-selected (long life and few risks).

Tinkle (1969) suggested that short life expectancy exerts strong selection for early maturity, yet geckos mature rather early and live long lives. A consideration of clutch size may aid in understanding this phenomenon. Gekkonid lizards produce unusually low, fixed clutch sizes of one to two eggs per clutch. It is suggested that to compensate for a low (per clutch) reproductive effort, *C. brevis* has developed high longevity and multiple clutches. Two clutches per season would result in an annual reproductive effort of only four young, which is low when compared to short lived, temperate species. Multiple clutches and more eggs per clutch are characteristic of most short lived species that occur with *C. brevis* (*Urosaurus ornatus*, $\bar{x} = 6.3$, Fitch, 1970; *Uta stansburiana*, $\bar{x} = 3.8$, Tinkle, 1961, Irwin, 1965; *Sceloporus olivaceus*, maximum = 25, Blair, 1960; *Sceloporus magister*, $\bar{x} = 12.4$, Fitch, 1970; *Cophosaurus texana*, $\bar{x} = 5.0$, Johnson, 1960). Geckos are relatively long lived; therefore, each female ultimately produces a total number of young comparable to short lived, larger clutch species. In view of the characteristics, it is suggested that *C. brevis* is more K than r-selected. As a result of non-variable, small clutch size, the species has adapted by evolving high longevity, thus raising the total reproductive effort.

Thermal Ecology

Cowles and Bogert (1944) demonstrated that by behavioral means reptiles are able to maintain their body temperatures within a relatively narrow range. Although variance of temperature by a few degrees may be of minimal consequence to reptiles, most species prefer a certain range of temperatures. Bellairs (1970) has suggested that such temperatures provide the conditions under which chemical processes of the body work most efficiently, and that the preferred body temperatures reflect the temperatures to which species are physiologically adjusted.

Environmental temperature variation imposes a daily cycle of activity on reptiles and methods by which reptiles control body temperature are quite diverse. Most typical is the diurnal lizard that emerges in early morning to bask. When the lizard has warmed to a sufficient temperature, it goes about its daily activity. To aid in absorbing radiation, some basking species orient their bodies at right angles to the sun's rays (Bellairs, 1970) while other species rely on substrate temperatures to raise body temperatures for foraging activities. When afternoon temperature peaks are reached, they reduce activity and retire to cooler burrows (Milstead, 1957). Still other species have adapted by lying beneath the sand in early morning with only the head projecting. The sun warms the blood circulating in the large sinuses around the eyes and the lizards emerge when body temperatures reach a level sufficient for activity (Bogert, 1959).

Cowles (1940) classified different strategies of thermoregulation among reptiles. He referred to species that use direct solar radiation as heliotherms and used the term thigmotherm to describe species that regulate via ambient air or substrate. Cowles and Bogert (1944) observed that some heliothermic species have behavioral adaptations for absorbing heat from the substrate.

A series of temperatures of Coleonyx brevis collected in the spring of 1972 by Drs. James R. Dixon and Fred S. Hendricks revealed that geckos under cover had body temperatures considerably higher than air or substrate temperatures. From those and subsequent data an analysis of the diel thermal ecology of that species was conducted.

Thermoregulation During Daytime

Field data on C. brevis collected under cover during the daytime (Table 4, Fig. 17 and 18) reveal that cloacal temperature versus air temperature and cloacal temperature versus substrate temperature are correlated. However, the comparison of cloacal temperature versus underside of cover temperature (Fig. 19) is more highly significant (cloacal versus air, r = 0.845; cloacal versus substrate, r = 0.881; cloacal versus cover, r = 0.897). Data for Figures 17, 18 and 19 were collected in spring and early summer.

On 23 June 1973, at Black Gap Wildlife Management Area, Brewster County, Texas, the environmental and body temperatures of one C. brevis were monitored for approximately eight hours and the

Table 4. Data on cloacal, air, substrate, and underside of cover temperatures and type of cover for <u>Coleonyx</u> <u>brevis</u> collected under cover. Temperatures are in °C.

Cloacal Temperature	Air Temperature	Substrate Temperature	Underside of Cover Temperature	Type of Cover
20.6	16.0	18.0	----	Rock
20.2	16.0	18.0	----	"
16.4	16.0	15.8	----	"
18.8	17.2	14.5	----	"
12.5	17.2	16.5	----	"
31.6	24.4	23.0	----	"
25.4	26.6	27.2	----	"
27.5	21.4	23.6	----	"
23.4	19.6	19.6	----	"
27.0	21.8	24.0	----	"
26.8	21.0	21.0	21.0	"
24.4	19.0	19.4	19.5	"
29.2	20.5	25.5	24.5	"
18.8	17.8	17.8	19.0	"
15.4	17.5	15.2	----	"
22.2	20.4	20.2	22.6	"
19.4	20.8	18.0	22.0	"
32.8	28.0	27.0	35.0	Plywood
30.2	28.6	25.4	31.6	"
30.8	29.6	28.2	31.0	Tar Paper
28.2	28.6	31.0	35.8	"
33.6	31.0	27.0	32.1	Cardboard
32.4	30.4	31.0	34.2	Tin
36.2	36.0	37.2	37.8	Rock
20.5	16.8	22.5	19.6	"

Table 4. (continued)

Cloacal Temperature	Air Temperature	Substrate Temperature	Underside of Cover Temperature	Type of Cover
24.8	20.8	22.4	----	Rock
24.0	20.8	24.0	----	"
24.4	23.4	23.4	----	"
23.6	23.4	23.4	----	"
20.9	20.2	20.6	----	Fallen Yucca
23.0	24.0	19.0	20.5	Tin
21.0	21.0	18.5	----	Rock
21.0	24.5	20.0	21.0	"
28.0	26.0	----	28.0	"
29.4	33.8	27.3	29.6	"
30.2	28.0	26.6	31.0	"
30.2	28.3	26.8	32.4	"
31.6	----	28.2	31.8	"
32.2	31.2	28.8	33.9	"
15.4	----	----	19.0	"
21.1	----	----	21.1	"
31.7	----	----	32.0	"
21.0	----	18.5	----	"
31.6	----	29.2	----	"

Figure 17. Regression comparing cloacal temperature and air temperature of _Coleonyx_ _brevis_ collected during daytime under cover. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.845 is significant at the $p < .01$ level.

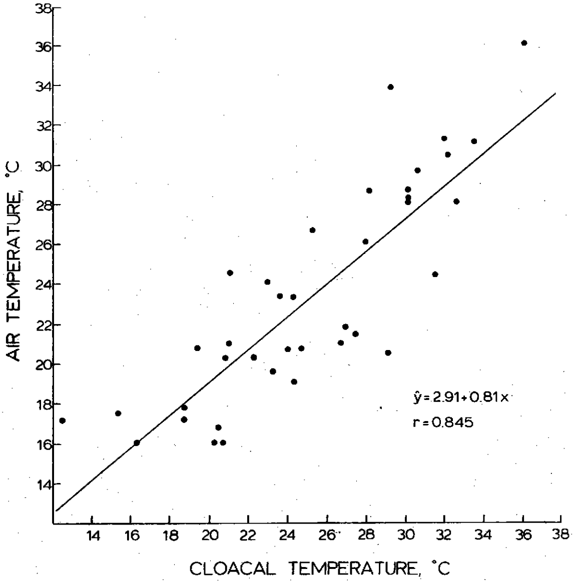

38
36
34
32
30
28
26
24
22
20
18
16
14
AIR TEMPERATURE, °C
14
16
18
20
22
24
26
28
30
32
34
36
38
CLOACAL TEMPERATURE, °C
ŷ=2.91+0.81x
r=0.845

Figure 18. Regression comparing cloacal temperature and substrate under cover temperature of Coleonyx brevis collected during daytime under cover. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.881 is significant at the $p < .01$ level.

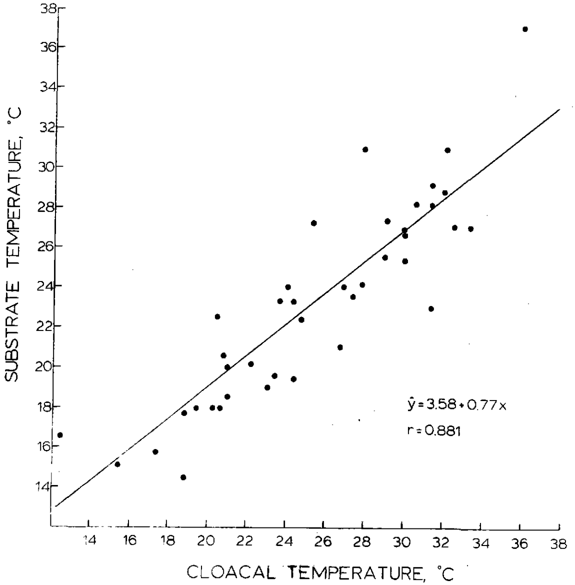
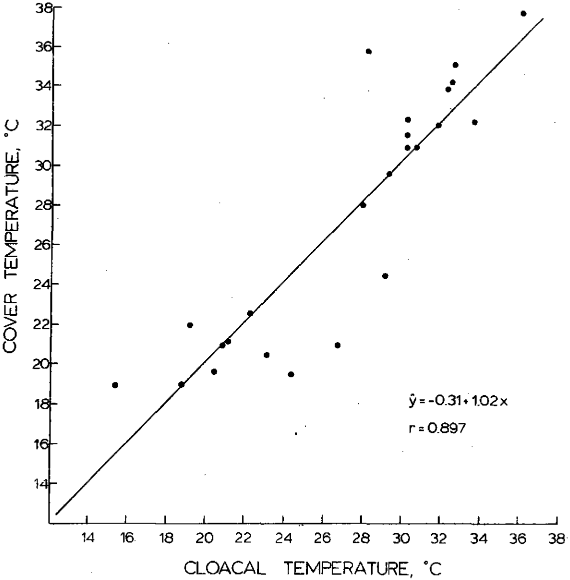

SUBSTRATE TEMPERATURE, °C
38
36
34
32
30
28
26
24
22
20
18
16
14
14
16
18
20
22
24
26
28
30
32
34
36
38
CLOACAL TEMPERATURE, °C
ŷ = 3.58 + 0.77x
r = 0.881

Figure 19. Regression comparing cloacal temperature and underside of cover temperature of Coleonyx brevis collected during daytime under cover. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.897 is significant at the $p < .01$ level.


COVER TEMPERATURE, °C
CLOACAL TEMPERATURE, °C
38
36
34
32
30
28
26
24
22
20
18
16
14
14
16
18
20
22
24
26
28
30
32
34
36
38
$\hat{y} = -0.31 + 1.02x$
$r = 0.897$

data are presented in Table 5.

Data from an experimental chamber (Table 6 , Fig. 20 and 21) supplement field data on thermoregulation. Twelve geckos were used, one per test. Coleonyx brevis were introduced into the chamber and allowed to explore the surroundings; usually within two minutes, geckos sought cover under the rock. In nine cooler tests, cloacal and cover temperatures were strongly correlated ($r = 0.922$, $p \leq 0.01$) while cloacal and substrate temperatures were not correlated ($r = 0.624$). In three warmer tests, cloacal temperatures approximated both air under rock and substrate temperatures.

Thermoregulation During Nighttime

During the summer of 1973, cloacal, air, and substrate temperatures were recorded for 51 C. brevis (Table 7, Figs. 22 and 23) active from 2130 to 0150 hours and four C. reticulatus (Table 8) active from 2310 and 0110 hours. For C. brevis, cloacal versus substrate temperature ($r = 0.918$) is more correlated than cloacal versus air ($r = 0.846$). Air temperature at sunset varied from 23° to 32°C, while substrate temperatures were always warmer, varying from 26° to 35°C. Coleonyx brevis were observed first immediately after sunset.

The lowest cloacal temperature at which C. brevis was active at night was 24.1°C. Earlier that night rains had cooled the air

Table 5. Data on cloacal, underside of rock, substrate under rock, and air under rock temperatures of Coleonyx brevis monitored in the field. Temperatures are in °C.

Time	Position of Gecko	Cloacal Temperature	Rock Temperature	Substrate Temperature	Air Under Cover Temperature
1430	Between rock and substrate	27	31	29	28
1630	Touching rock and substrate	28	33	29	27
1830	Appressed to substrate	29	31	29	28
2030	Elevated to rock	29	29	30	24
2230	Appressed to substrate	28	25	30	25

Table 6. Data from laboratory tests of *Coleonyx brevis* thermoregulatory behavior under cover. Temperatures are in °C.

Test	Cloacal Temperature	Cover Temperature	Substrate Temperature	Position of Gecko
Tests with substrate temperatures <24°C				
1	29.0	30.0	19.0	Appressed to cover
2	27.0	30.0	17.0	"
3	31.5	33.0	23.0	"
4	28.5	31.0	20.0	"
5	27.0	29.0	17.0	"
6	27.5	29.0	20.0	"
7	27.0	29.0	19.0	"
8	26.0	28.5	19.5	"
9	27.5	30.0	22.0	"
Tests with substrate temperatures >24°C				
1	32.0	34.0	26.5	Between cover and substrate
2	30.5	35.5	27.0	Appressed against substrate
3	30.5	34.5	27.0	Between cover and substrate

Figure 20. Regression comparing cloacal temperature and substrate temperature of Coleonyx brevis tested in the laboratory for thermoregulatory behavior under cover. Experiment represents nine tests where substrate temperatures were less than 24°C. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.624 is not significant at the $p < .01$ level.

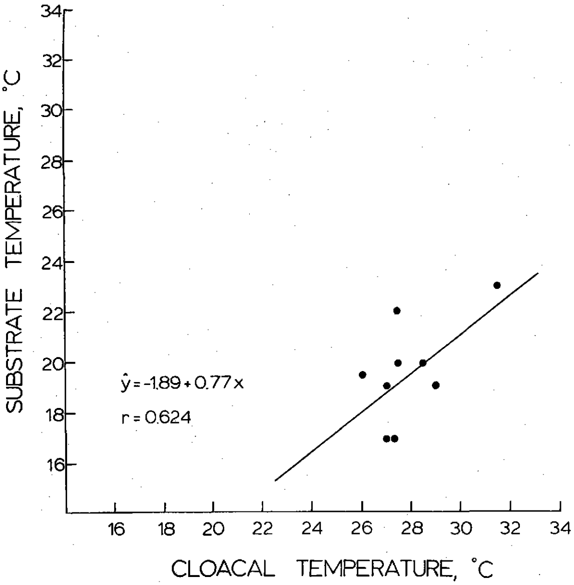

SUBSTRATE TEMPERATURE, °C
34
32
30
28
26
24
22
20
18
16
$\hat{y} = -1.89 + 0.77x$
r = 0.624
16
18
20
22
24
26
28
30
32
34
CLOACAL TEMPERATURE, °C

Figure 21. Regression comparing cloacal temperature and underside of cover temperature of Coleonyx brevis tested in the laboratory for thermoregulatory behavior under cover. Experiment represents nine tests where substrate temperatures were less than 24°C. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.922 is significant at the $p < .01$ level.

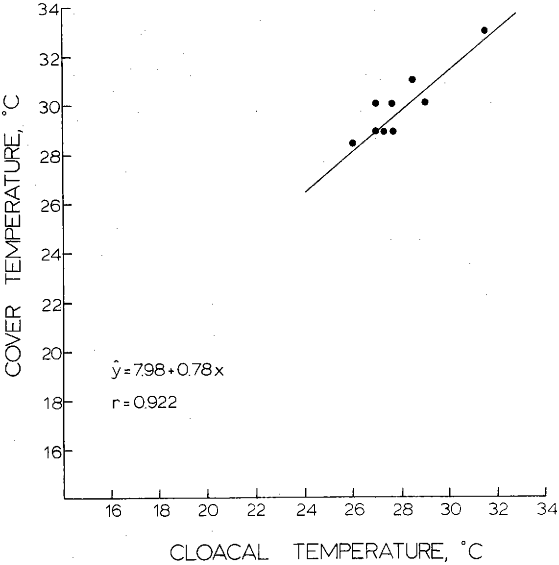

34
32
30
28
26
24
22
20
18
16
COVER TEMPERATURE, °C
ŷ = 7.98 + 0.78 x
r = 0.922
16
18
20
22
24
26
28
30
32
34
CLOACAL TEMPERATURE, °C

Table 7. Data on cloacal, air, and substrate temperatures of *Coleonyx brevis* collected while active on paved roads and the desert floor at night. Temperatures are in °C.

Cloacal Temperature	Air Temperature	Substrate Temperature
24.1	21.8	24.9
24.2	23.0	24.3
24.2	23.9	25.6
24.4	27.2	24.0
25.6	24.8	25.8
25.8	23.1	26.1
26.2	23.0	26.2
26.2	23.6	26.4
26.2	24.6	27.1
26.2	24.8	27.2
26.4	24.8	28.6
26.6	24.0	29.4
26.8	23.9	26.8
27.2	26.8	26.0
27.2	27.4	27.4
27.4	26.8	----
27.5	24.9	28.2
27.8	24.2	28.4
27.8	26.0	28.8
27.8	26.8	29.1
28.7	25.7	30.6
28.7	26.9	31.0
28.8	26.7	30.1
29.0	25.8	30.2
29.0	29.0	32.6
29.1	26.4	30.0

Table 7. (continued)

Cloacal Temperature	Air Temperature	Substrate Temperature
29.4	25.8	29.0
29.8	28.1	32.2
30.0	28.7	30.8
30.2	26.7	30.2
30.2	27.8	33.1
30.4	26.7	32.8
30.5	26.1	31.0
30.7	28.0	31.6
31.2	28.7	32.4
31.4	31.2	33.2
31.6	29.4	32.0
31.6	30.2	33.6
31.8	30.2	33.2
32.2	29.8	33.8
32.5	29.3	32.3
32.4	30.4	33.6
32.2	31.6	34.2
32.3	32.5	35.3
32.9	31.4	34.3
24.8	23.2	26.8
26.7	25.2	26.9
26.8	26.2	28.2
28.0	24.8	31.0
30.0	31.8	34.4
31.9	28.4	31.9
27.2	31.3	31.3

Figure 22. Regression comparing cloacal temperature and air temperature of Coleonyx brevis active at night. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.846 is significant at the $p < .01$ level.

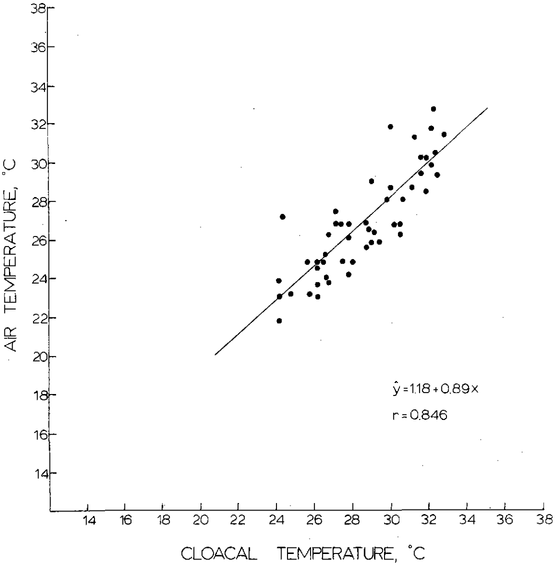

38
36
34
32
30
28
26
24
22
20
18
16
14
AIR TEMPERATURE, °C
14
16
18
20
22
24
26
28
30
32
34
36
38
CLOACAL TEMPERATURE, °C
ŷ = 1.18 + 0.89x
r = 0.846

Figure 23. Regression comparing cloacal temperature and substrate temperature of Coleonyx brevis active at night. Regression estimate and correlation coefficient are given. Correlation coefficient of +0.918 is significant at the $p < .01$ level.

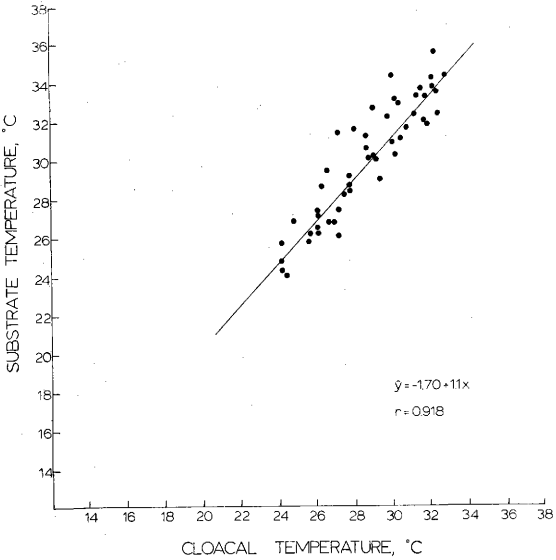

SUBSTRATE TEMPERATURE, °C
38
36
34
32
30
28
26
24
22
20
18
16
14
14
16
18
20
22
24
26
28
30
32
34
36
38
CLOACAL TEMPERATURE, °C
ŷ = -1.70 + 1.1x
r = 0.918

Table 8. Data on cloacal, air, and substrate temperatures of *Coleonyx reticulatus* collected while active on paved roads at night. Temperatures are in °C.

Cloacal Temperature	Air Temperature	Substrate Temperature	Climatic Conditions
31.7	28.9	32.1	Rain
24.5	23.5	27.0	Rain
29.2	25.6	26.8	Rain
26.0	19.8	22.4	Rain
----	23.0	----	Rain

(21.8°C) and ground (24.8°C) considerably and very few C. brevis were active. However, many more C. brevis were collected on nights when substrate temperatures were greater than 28°C. The highest cloacal temperature at which C. brevis was active was 32.9°C; air and substrate temperatures were 31.4° and 35.6°C, respectively.

Temperature Preferences

Thermal preferences were determined by testing each species in a thermal gradient. Geckos were introduced into the gradient at nighttime and explored the surroundings slowly. Frequently, geckos would move under cover items, but soon would move out and continue exploration. Eventually, all geckos tested came to rest under cover. Temperatures were recorded in the mornings. Of 14 C. brevis tested two times each, mean cloacal temperature was 31.6°C (±2.19; Table 9); of two C. reticulatus, one tested seven and one tested eight times, mean cloacal temperature was 26.0°C (±2.22; Table 9). A t test showed the two means to be significantly different at the 0.01 level ($t = 7.8865$, 41 d.f.).

Thermal Strategy

Field data collected in spring and early summer indicate that during the day C. brevis behaviorally thermoregulate below cover items. Parker and Pianka (1974) showed a correlation between cloacal and air temperature in C. variegatus and Licht et al., (1966)

Table 9. Preferred cloacal temperatures of *Coleonyx brevis* and *Coleonyx reticulatus* in a laboratory thermal gradient. In parentheses, mean temperature is followed by standard deviation. Diferences in means are significant at the $p \leq .01$ level ($t = 7.8865$, 41 d.f.). Temperatures are in °C.

Coleonyx brevis ($\bar{x} = 31.6$, ±2.19)		*Coleonyx reticulatus* ($\bar{x} = 26.0$, ±2.22)	
Specimen No.	Cloacal Temperature	Specimen No.	Cloacal Temperature
1	33.0	1	28.5
	29.5		27.5
2	30.5		26.5
	32.5		29.0
3	33.5		28.0
	33.5		24.0
4	32.5		23.5
	31.5		
5	34.0	2	26.5
	31.0		29.0
6	28.0		24.5
	26.0		24.5
7	30.0		25.5
	31.0		23.0
8	31.0		27.5
	32.0		22.5
9	31.0		
	34.5		
10	29.0		
	34.0		
11	33.5		
	33.0		
12	34.5		

Table 9. (continued)

Coleonyx brevis ($\bar{x}$ = 31.6, ±2.19)		*Coleonyx reticulatus* ($\bar{x}$ = 26.0, ±2.22)	
Specimen No.	Cloacal Temperature	Specimen No.	Cloacal Temperature
	31.5		
13	31.5		
	27.0		
14	31.5		
	33.5		

observed that in some species of Australian geckos daytime body temperatures were as high as in diurnal species. However, the authors did not determine if the lizards were actively thermoregulating or passively assuming microenvironmental temperatures. Data in this thesis and that of Dixon and Hendricks (unpub. data) suggest that in the daytime during spring and early summer, C. brevis behaviorally thermoregulate by conduction from cover items as well as from substrate and surrounding air (Fig. 19, p. 79). Of particular interest is a three day period in early spring when nighttime temperatures fell to 0°C. During the day solar radiation raised cover temperatures considerably higher than substrate and air temperatures. On those days cloacal and cover temperatures were almost identical and much warmer than substrate and air temperatures.

On 23 June 1973, one C. brevis being monitored was observed altering its body position to raise and lower its body temperature. During the day the gecko was elevated on all legs, intermediate in position between the substrate and the rock. Substrate and rock temperatures were considerably high (29° and 31°C, respectively). However, cloacal and air temperatures were lower (27° and 28°C, respectively). At sunset, the gecko was observed elevated and in contact with the rock; cloacal and rock temperatures were identical (29°C), substrate temperature was higher (30°C), and air temperature was much lower (24°C). At late night, the gecko was observed resting with the venter to the substrate; air and rock temperatures were low (25°C) but cloacal and substrate temperatures were high (28° and 30°C, respectively).

In the laboratory, _C_. _brevis_ were observed thermoregulating by raising their bodies to contact warmer cover items. In nine "springtime" condition tests (substrate <24°C), geckos were elevated on all legs and the dorsal surfaces of their bodies were in contact with the rock (Fig. 24). Approximately two minutes elapsed from the time a gecko first moved under the rock to when it first elevated its body. The geckos remained elevated for approximately 10 to 12 minutes. After warming, geckos would lower their bodies to an intermediate position between the rock and the substrate and if cold substrate conditions continued geckos would elevate and bring their bodies back into contact with the rock.

In three "summertime" condition tests (substrate >24°C), geckos remained in a position intermediate between the rock and the substrate. Cloacal and substrate temperatures were almost identical but rock temperatures were much warmer and contact with the rock was avoided.

These data support field data suggesting that the species does behaviorally thermoregulate during the day via altering body position into contact with cover items, substrate, and air to assume the desired temperature. During spring, and possibly fall, when

Figure 24. Adult *Coleonyx brevis* actively thermoregulating by raising the body into contact with a warmer cover item (rock). The tests revealed that *C. brevis* raise and lower the body between substrate and cover items to regulate body temperatures.

FIGURE 24

environmental temperatures are low and solar radiation raises cover temperatures, geckos position themselves under cover to raise body temperatures. During summer, when surface temperatures are lethal, geckos probably seek the coolest microhabitats available. It was observed that geckos collected below large rocks and dug out of crevices in the summer were cooler than surface substrate temperatures.

All of the geckos collected at night were out in the open. Most geckos were lying still when first observed but some were actively prowling and attempted to flee when approached. Apparently, active geckos depend mainly on the substrate for warmth. Dixon and Kroll (1972) suggested methods by which some species of *Phyllodactylus* in Peru test the substrate to detect drops in temperatures. In Peruvian deserts, substratum was shown to cool more rapidly at night than air. However, in North American deserts air temperatures drop rapidly while rock and substrate loose heat slowly. *Coleonyx brevis* may absorb substrate heat by periodically resting with the venter touching the substrate. Possibly such a technique is used during feeding periods as data presented elsewhere in this thesis indicate that geckos frequently "sit and wait" while actively searching for food. This method may be used in maintaining temperatures within a range preferred for activity.

Generally, nighttime activity periods for nocturnal lizards are restricted by temperature as are daytime activity periods for diurnal lizards. Though air temperature drops rapidly after sunset, substrate material remains warmer longer and activity continues to early and mid nighttime. When temperatures drop sufficiently, lizards retreat to shelter and activity ceases.

In C. brevis, cool temperatures (approximately 21°C) probably inhibit metabolic activity. It is suggested that daytime behavioral thermoregulation under cover is a method by which metabolic activity is increased. Altering body position enables C. brevis to maintain body temperature within an optimal range. Such behavior serves to maximize the efficiency of the digestive process. A precise definition of the temperature range and data on the physiology of the metabolic process in relation to temperature must await further study.

Bustard (1967) described behavioral thermoregulation under bark in the arboreal species Gehyra variegata. He demonstrated that Gehyra alters body position laterally under bark on standing trees, to and away from the sun, to maintain body temperature. However, Gehyra does not raise or lower the body. The method described for Gehyra is ideal for an arboreal species, while the technique described in Coleonyx seems appropriate for terrestrial life.

Werner and Broza (1969) suggested that in two ground dwelling genera, Stenodactylus and Ceramodactylus, the semi-erect and erect position serves to extend the range of vision while the geckos are foraging. He also noted that captive Ceramodactylus occasionally rest in the semi-erect or erect position under cover for up to 30 minutes. Werner (1969) stated that the semi-erect and erect positions are evoked by thigmotaxis, with the dorsum being appressed to the ceiling of the retreat. Werner (1969) included a photograph of a gecko under cover in that position and it is remarkably similar to the thermoregulatory position of C. brevis. In terrestrial species of geckos the function of the elevated position may be two-fold, to increase the range of vision while prowling and to thermoregulate while under cover.

Extensive studies of the thermal ecology of reptiles indicate that most species prefer body temperatures within a restricted range. However, available temperatures do not always coincide with the preferred range and activity is strongly governed by environmental temperatures. Licht et al., (1966) have shown that variance in body temperature in nature is usually greater than variance as determined in a thermal gradient. Pianka and Pianka (1970) suggested that such variation reflects a variety of ecological activities. Ranges of temperature in the field probably also represent a compromise between available temperature and preferred temperature. In this thesis, field data show that at night body temperatures of C. brevis average approximately 29°C. Few data are available for daytime summer temperatures, but laboratory data suggest that C. brevis prefers and maintains temperatures from 31° to

32°C; temperatures recorded in the thermal gradient support this ($\bar{x}$ = 31.6°C). Of the 28 tests, 23 temperatures were 30°C or greater. Geckos were usually in this temperature range both day and night, suggesting that lower environmental temperatures in the field at night are indeed less than the preferred temperature and do represent a compromise in exchange for nocturnal activity.

Diet Composition

An analysis of stomach contents of *Coleonyx brevis* reveals that the species is a fairly generalized feeder, taking a wide variety of prey; Table 10 summarizes stomach contents of *C. brevis*. Almost all stomachs examined contained food. Predominate prey items were termites (Isoptera) and cicadellids (Homoptera). Spiders, solpugids, crickets, and moths comprise a considerable part of the diet. Other prey items, such as mirids (Hemiptera), are common in numbers but total little in volume.

The significance of the analysis is that *C. brevis* apparently actively forages for food in a variety of microhabitats. Certain insect families and their respective species in the diet of *C. brevis* (Cicadellidae, Miridae, Tingidae) are found only on plant leaves and stems (mirids are found commonly on stems, tingids only on the underside of leaves, and cicadellids on both stems and leaves). Those insects rarely leave their respective microhabitats. Rather, they are quite cryptically patterned and usually rely on

Table 10. Summary of stomach contents of 59 Coleonyx brevis and five Coleonyx reticulatus. Specimens were collected in June and July, 1972 and 1973 at Black Gap Wildlife Management Area, Brewster Co., Texas. Volumes are in cc.

Species	Order	Family	Number	Volume
Coleonyx brevis	Araneae		18	0.30
	Acarina		9	0.04
	Solpugida		6	0.30
	Chilopoda		1	0.01
	Scorpionida		1	0.01
	Collembola	Smithurnidae	1	0.01
	Orthoptera	Mantidae	2	0.03
		Gryllidae (adults & nymphs)	15	0.20
		Tettigoniidae (nymph)	2	0.10
		Blattoidea (superfamily)	1	0.09
		Acridae (nymph)	5	0.10
	Thysanura	Machilidae	1	0.03
		Lepismatidae	1	0.01
	Isoptera	Termitidae (workers)	150	1.12
		(winged adults)	47	0.80
	Lepidoptera	Noctuidae	3	0.20
		Geometridae (larvae)	2	0.03
		Pyralidae	2	0.20
		Unidentified (larvae)	6	0.20
	Homoptera	Pseudococcidae	2	0.02
		Cicadelidae	70	0.50
	Hemiptera	Miridae	12	0.02
		Tingidae	1	0.01
		Lycaeidae	2	0.02
		Reduviidae	1	0.01

Table 10. (continued)

Species	Order	Family	Number	Volume
	Hymenoptera	Formicidae	7	0.10
	Coleoptera	Tenebrionidae	3	0.10
	Diptera	Nematocera (suborder)	1	0.01
		Syrphidae	2	0.02
		Sciaridae	1	0.01
		Pipunculidae	1	0.01
Coleonyx _reticulatus_	Orthoptera	Acrididae	1	----
	Coleoptera	Tenebrionidae	3	----
	Aranae		1	----
	Plant (composite)		--	----

remaining still to avoid predation. That one specimen of gecko had 20 cicadellids in its stomach indicates that the lizards are indeed actively foraging among plants, rather than occasionally encountering them as the lizards prowl. The insects possibly are being taken on low spreading, decumbent vegetation as such plants are common in areas where the geckos were collected. On several occasions, _C_. _brevis_ were observed moving about slowly among such plants, but it was not noticed if the geckos were actually feeding from the plants.

Of additional interest are the data regarding termites as prey items. Termites comprise the single most important prey item (volume and number) of _C_. _brevis_ during June and July. Both workers and winged adults were eaten by _C_. _brevis_. Workers were the most common food item in stomachs and comprised the largest total volume. Workers are found only in termite nests or in termite "runs," which extend several directions from the nests. Frequently, termite "runs" were observed under small sticks, larger fallen vegetation, and rocks which were turned. When exposed, workers quickly sought shelter by escaping back into the soil. The fact that workers were commonly found in the stomachs of _C_. _brevis_ indicates that the geckos actively forage by turning small sticks or digging to get termites. By either behavior a gecko could come across termite "runs" and rapidly gorge itself without much effort; one specimen contained 83 tightly packed workers.

Winged adults comprised approximately one third of the total termite composition and well over one half the total volume. Swarming in winged adult termites is initiated by rains and usually occurs at night during the season. At Black Gap Wildlife Management Area all winged adults were found in stomachs of geckos collected on one night (15 June 1973). Rains had fallen from sunset to approximately 2330 hours. Apparently, the termites were swarming and geckos were capturing them at the surface of the ground. On another occasion preceded by rain (20 June 1973) in Val Verde County, Texas, two geckos were collected with winged adults in their stomachs.

Most other prey could be encountered while geckos are active on the desert floor as some beetles, ants, spiders and solpugids are nocturnal.

Data on feeding behavior in the laboratory reveal that _C. brevis_ has a rather eclectic approach to feeding utilizing both olfactory and visual cues to detect prey. That so many cryptic forms of insects (Homoptera and Hemiptera) were eaten supports the data regarding chemoreception in feeding (see Feeding Behavior, p. 119). Likewise, _C. brevis_ may use chemical cues in locating termites. It is likely that geckos, while turning sticks or digging, could chemically detect termite allomones and would probably examine such areas closely. However, such speculation must await further investigation.

Different strategies on diet diversity and the amount of energy expended in searching for food have been eloquently discussed by MacArthur and Levins (1964) and MacArthur and Pianka (1966). MacArthur and Levins (1964) discussed "fine-grained" species (those that utilize all resources in the proportion in which they occur) and "coarse-grained" species (food specialists). Of the former they indicated that species that spend most of their time searching, especially for small items, cannot afford to overlook many different kinds of prey. Hence, species with relatively short search times will tend to take most prey encountered, steering away from food specialization. MacArthur and Pianka (1966) listed several factors that favor specialization in diet and among them was decreased environmental resistance to movement.

Nocturnality probably restricts activity of C. brevis considerably; activity occurs from sundown to when temperatures are too low for activity, usually around 2400 hours. Hence, C. brevis has a reduced time in which to complete activity. It is suggested that C. brevis is a rather finely-grained species, taking most prey encountered, rather than specializing on one prey type. Low temperatures serve to increase environmental resistance to movement (in the sense of MacArthur and Pianka, 1966) and as suggested by MacArthur and Levins (1964) for a "fine-grained" species, most of the prey items taken by C. brevis are rather small, averaging approximately 0.01 cc (Table 10, p. 105). The species utilizes visual and chemical components of the senses to detect prey which aid in capturing as many prey items as possible. Stomach content analysis of C. brevis supports this: at least 29 families of 15 orders were taken and many were cryptically patterned forms that were probably detected by chemoreception.

Three stomachs and two defecations of C. reticulatus were analyzed (Table 10). One stomach was empty, one contained two plant parts (a composite), and one contained remains of a spider. The two defecations were collected from specimens collected in the summer of 1973, and each was the first defecation in captivity for each specimen. Parts of one grasshopper and three tenebrionid beetles were found.

Other Aspects of Behavior

Exploratory behavior. Both species of geckos are rather slow, casual prowlers. When introduced into terraria in daylight, both move about searching for cover and take shelter under cover items immediately, while at night both move about slowly when exploring surrounding. Investigative movements are accompanied by frequent tongue flicks to new surfaces. Typical of the behavior of both species is the following account. On 2 July 1973, at 2300 hours, a large male Coleonyx reticulatus was introduced into the center of a terrarium (ambient air temperature = 25°C). After 30 seconds the lizard moved slowly towards one corner of the terrarium.

Movement to the corner took approximately 1.5 minutes, during which time the lizard stopped frequently, extending its tongue to substrate, rocks, and the wall of the terrarium twelve times.

Slow exploratory movements of Coleonyx are unlike most other desert terrestrial species (Urosaurus, Cophosaurus, Cnemidophorus). Frequent tongue flicks may represent attempts to chemically "analyze" the objects. Slow movements may serve to attract predators less often than do quick, jerky movements.

Walking. Both species walk in an elevated position with the angle of the humerus and radius approximately 45°. In walking, the left front leg is moved forward followed immediately by the right rear leg. After a slight interval, the right front leg is moved forward followed immediately by the left rear leg. During the process the body is arched alternately to the right and left, the side corresponding to the rear leg being moved. The tail is carried at the height of the body, laterally curved and parallel to the ground.

Digging. The following account is typical of digging behavior of both species. A large C. reticulatus was introduced into a terrarium with sand-gravel substrate and one cover item (plexiglass) positioned flush with the substrate. After moving about for approximately five minutes, the lizard began exploring the edge of the cover and began digging by reaching under the cover with the left forelimb and pulling back substrate eight times. Next, it reached forward with the right forelimb and pulled back substrate five times; then, it inserted its head into the burrow and pushed forward. Time elapsed to this point was 1.5 minutes. The lizard moved away from the burrow for three minutes, returned, and resumed the same digging pattern until the burrow was large enough for the front half of its body to enter. With one half of its body in the burrow, it pushed substrate away from the sides of the burrow, moved away for two minutes, and returned. It continued the digging pattern, alternating the forelimbs with eight to ten strokes each and the hindlimbs with six to eight strokes each. Occasionally, during the process, it pushed forward with its body and at all times while digging, its body was lifted up off the substrate in the prowling stance. After removing enough substrate for entry, it curled its body in the burrow.

Digging behavior in Coleonyx is similar to that of other terrestrial species. Climatic conditions in the desert are such that escape into the ground is essential, especially for nocturnal species. Coleonyx brevis is most common in areas with gravelly soil interspersed with large rocks. Both species can dig in gravelly soil well and may take advantage of crevices between rocks, also. Coleonyx brevis has been collected in burrows under rocks and in crevices between rocks. The species can be found under rocks on sunny, warm days in winter and spring, or on overcast days in summer: all specimens collected in crevices were found during the summer. Temperatures in burrows immediately below rocks on sunny summer days are probably too high for Coleonyx brevis, since none was found there.

Aggregation. Frequently, when several specimens were kept together, males and females were found under common cover items, but occasionally a single specimen, usually smaller, would burrow under the water dish or a rock. Greenburg (1943) suggested that aggregation during the nonbreeding season was advantageous to nocturnal species. Furthermore, he demonstrated that dispersal factors come into action during the breeding season of C. variegatus. However, captive specimens of C. brevis showed aggregation tendencies throughout the year.

As in most species of lizards, both species demonstrated thigmotaxic responses to cover items. Preferred resting positions were located where the lizards were in contact dorsally with the cover items and laterally with the cover supporting items.

Climbing. Both species possess the ability to climb; however, the behavior is more developed in C. reticulatus. In the laboratory, both specimens of C. reticulatus were observed climbing on sticks. Frequently, the large C. reticulatus climbed on an eight inch dried piece of ocotillo, which was arranged extending out of the substrate at a 60° angle to approximately seven inches from the top of the terrarium. On one occasion the lizard escaped, probably by climbing to the top of the stick and jumping to the edge of the terrarium.

On another occasion the small C. reticulatus escaped probably by climbing a 4 mm diameter telethermometer cable extending from the substrate to the top of the terrarium. The escape was not observed; however, the lizard demonstrated an ability to cling to and climb the cable at a later date.

Both specimens of C. reticulatus possess prehensile abilities in their tails. The smaller specimen has the original tail and frequently uses it for partial support when climbing in one's hand and on other objects. The larger specimen has a regenerated tail but is capable of curving it partially around objects while climbing. The prehensile quality is similar to that observed in Gerrhonotus liocephalus and reported for other species of Gerrhonotus (Stebbins, 1966).

Data suggest that C. reticulatus is at least partially arboreal. It is possible that the species takes advantage of yuccas, shrubs, and cacti by feeding and finding shelter above the ground. An analysis of stomach contents may support this.

Defensive behavior. An adult specimen (320 mm - total length) of Hypsiglena torquata texana (a natural predator of C. brevis) was used to study prey reaction of Coleonyx. In each of the five tests on C. brevis, as the snake slowly approached the gecko, the gecko would position itself at right angles to the snake and remain motionless, except for arching and waving its tail. When the snake was within at least four cm of the gecko, the gecko would flee.

In each of two tests, when the snake was allowed to approach _C_. _reticulatus_, the gecko reacted by fleeing rapidly. Flight occurred when the snake was as close as seven cm. No tail waving was observed in this species.

Coleonyx _brevis_ probably uses tail waving to distract predators as geckos that were in the presence of snakes remained motionless except for tail waving. Possibly, predator attention is directed to the tail and away from more vital parts of the body.

Pianka (1970a) showed a relationship between tail breakage and predation pressure in _Cnemidophorus_ _tigris_ and the percentage of regenerated tails is probably an accurate estimate of predation in other lizard species as well. Table 11 presents data, by sex, on percentages of naturally occurring regenerated and complete tails in _C_. _brevis_ and _C_. _reticulatus_. In _C_. _brevis_, frequency of broken tails increases with size probably because older specimens have more contact with predators. Percentage of regenerated tails was higher in females than males and may indicate that females have more contact with predators than males. Possibly, because of the additional weight of eggs, gravid females move more slowly and rely on tail autotomy more often than males.

Table 11. Frequency of regenerated tails by size class and sex for specimens of *Coleonyx brevis* and *Coleonyx reticulatus*.

Species	Size Class	N	Number Regenerated	Percentage Regenerated
Coleonyx brevis				
	Juveniles (<45 mm)	27	13	48
	Males (>45 mm)	133	91	68
	Females (>48 mm)	96	77	80
Coleonyx reticulatus				
	Juveniles (44 mm)	1	0	0
	Males (>58 mm)	4	1	25
	Females (>58 mm)	9	5	55

Data on tail regeneration frequency in C. reticulatus are few but it seems likely that the species uses the tail for distraction of predators less frequently than C. brevis. Tail waving was observed only once, and not in a predator-prey relation. Most C. reticulatus bite vigorously when first collected and one specimen (Fred S. Hendricks, pers. comm.) secreted a pungent, viscous fluid when collected; no C. brevis attempted to bite when handled. Tails of living C. reticulatus seem less fragile, are partially prehensile, and are very slim in comparison to the apparently more steatocaudic C. brevis; they appear quite different in gross structure and it is probable that a different strategy of tail use is involved. The more aggressive nature of C. reticulatus may aid in defense against predators, while the smaller, more docile C. brevis probably depends on predator distraction by tail waving. An aggressive species would depend less on tail autotomy and the species could develop other adaptations regarding the tail, such as arboreality.

Parker and Pianka (1974) suggested that C. variegatus mimic scorpions by tail waving. Indeed, Coleonyx is colored as a scorpion and the arched tail resembles the postabdomen and barb. However, it seems that predators seeing the mimic barb would avoid it and attack the head of the "scorpion," the vulnerable part of the gecko. If mimicry acts as a delay mechanism enabling geckos to escape, few attacks on tails would occur. Furthermore, if predators avoid scorpions and scorpion mimics altogether, few attacks on tails would occur, reducing the frequency of regenerated tails in *Coleonyx*. Data indicate high frequency of tail regeneration in *C. brevis*.

Territoriality. Little territoriality was observed in *C. brevis*. In captivity, males were frequently found with other males under common cover items and rarely was a male seen displaying to another male by arching its back; no fighting was observed. During feeding, larger specimens appeared more aggressive than smaller ones and usually captured more prey.

Territoriality in *C. reticulatus* was demonstrated nicely when the two males were put together. In one experiment, the larger specimen was introduced into the opposite end of the terrarium from the smaller. The larger (A) began to explore the surroundings, frequently tonguing the substrate; the smaller (B) saw A and began slowly waving its tail (not in the arched and curled position of *C. brevis* defensive behavior); A approached B; B arched its back and A remained in a walking stance; B expanded its throat, similar to the behavior described by Greenburg (1943) for *C. variegatus*; the two met and tongued the side of the other's head four to five time; B positioned itself parallel to A and crawled across A's head, dragging its anus across the top of the head; B moved away; A approached B and B arched its body and turned it so that the ventral and lateral parts were exposed to A; again

B expanded its throat; again they tongued each other's head; A moved away. Three minutes later A approached B; A examined the anal region of B; B wrapped its tail partially around A's head; A moved away. After two minutes A approached B and examined B's tail; B lashed its tail and moved away.

The territoriality displayed by *C. brevis* is similar but less intense than described for *C. variegatus* (Greenburg, 1943); neither rushing at the opponent nor biting was observed. In *C. brevis*, subordinates moved away after dominants approached; dominants were always larger specimens. Some aspects of territoriality in *C. reticulatus* are similar to *C. variegatus*. However, most segments of the behavior are quite different and may reflect a combination of territoriality and precopulatory behavior. The inability of the smaller to displace the larger when display occurred probably indicates that size is important in establishing territory.

Feeding behavior. The experiments with neonate *C. brevis* revealed very little regarding the innate ability of geckos to detect prey chemoreceptively. Hatchling geckos were very cautious of any movement around them. When cotton swabs were presented, the subjects reacted by moving away rapidly, leaving little chance for them to detect the presence of the extract. When the extract was dabbed on the labials, labial licking followed with four to five consecutive licks occurring under one eye, around the front of the mouth, and under the other eye. With each lick, the tongue was extended slightly and curled up over a labial, then pulled back into the mouth and re-extended to the next labial.

The experiments on chemoreception in adults revealed that C. brevis can detect prey items by chemoreception. When a swab dipped in distilled water was presented to a subject 10 mm in front of its mouth, the gecko would tongue it once or twice but would appear uninterested and move away. When a swab with distilled water was touched to the labials, the gecko would lick its labials to remove the water. When a swab dipped in fluid from crushed mealworms was presented to a subject 10 mm in front of its mouth, the gecko would tongue the swab and react with interest. If a swab was moved away slowly, the gecko would pursue the swab and prey-attack behavior occurred when a swab was held in one place. Of four tests (four subjects) four attacks were directed to the swab. Prey-attack behavior was characterized by the subject biting the "prey" in feeding response fashion and vigorously shaking the "prey" three to four times during which the subject's entire body was shaken and frequently lifted off the ground. This behavior was also observed while geckos were feeding on mealworms and crickets.

Observations in captivity indicate that both species somewhat actively forage for food. Occasionally during feeding, specimens would pause and then continue to prowl with caution. Pianka (1973) discussed the strategy involved in "sit and wait" and actively foraging techniques. Neither species of Coleonyx foraged as actively as did species of Ctenotus studied by Pianka (1969). However, neither did they passively "sit and wait" as is typical of many species of lizards. The strategy of both species seems to involve characteristics of both foraging techniques.

Visual stimuli are important in the feeding behavior of both species. In most feeding responses on whole prey items, visual stimuli proceeded prey-attack behavior and moving prey were pursued and captured more frequently than were dead prey. On receiving a visual stimulus of a live prey item, C. brevis would wave its tail slowly, perhaps to distract the prey. When the prey moved the gecko would pursue it and attack occurred only when the gecko was very close to the prey. Frequently, when the prey remained motionless, the gecko would approach, arch its head and neck above the prey, and strike downward. Tongue flicks did not occur when geckos were pursuing moving prey.

Coleonyx brevis approaches prey with a series of short runs while Coleonyx reticulatus approaches with slow, deliberate movements, moving one leg at a time, very slowly, until very close to the prey. Then, C. reticulatus arches the head and neck and lunges forward to capture the prey.

Attack on dead prey occurred rarely; both species paid little attention to dead prey. Frequently, a gecko approached a dead prey item and oriented to the item, but rarely did it attack. Apparently, visual stimuli are necessary to release prey-attack behavior.

Though visual stimuli are important, chemical stimuli are involved significantly. Stebbins (1948) indicated that Coleonyx have a keen sense of smell. In C. brevis, prey-attack behavior occurred on swabs dipped in prey body fluids. Tongue flicks to surrounding objects occur frequently and could represent an attempt to detect allomones left by passing prey. On one occasion an adult C. brevis, recently introduced into a terrarium in which geckos had been fed, was observed exploring the substrate with tongue flicks and at one point the gecko attacked the substrate by biting into it as if feeding. On another occasion Charles L. Simmons (pers. comm.) observed the large C. reticulatus pursuing a grasshopper that had climbed up the glass wall of a container. The gecko followed the trail the grasshopper had taken and attempted to climb the glass at the location the grasshopper had ascended. At no time after it had climbed the glass was the grasshopper visible to the gecko.

Occasionally, geckos lick the labials while exploring and more frequently after feeding. Harry W. Greene (pers. comm.) has suggested that such behavior removes chemical stimuli on labials that might mislead geckos while pursuing other prey items. It is possible that chemical signals aid geckos in trailing prey while visual stimuli are necessary to release approach behavior. Visual and chemical stimuli combined may be required to release the final prey-attack behavior. Another eublepharine, Eublepharis maculatus, was observed to approach a moving item (new born mouse), tongue it, and move away apparently failing to receive the correct chemical signal. If both stimuli are necessary, the removal of chemical signals from the labials by labial licking after feeding would be beneficial in preventing a gecko from attacking prey that satisfied only the visual component. An eclectic approach to feeding, combining two senses, may aid in preventing geckos from attacking harmful organisms.

Interspecific interference. When C. reticulatus approached C. brevis, C. brevis raised its tail and moved away; Coleonyx reticulatus appeared uninterested in C. brevis. In five out of eight tests on interference, each of the species occupied separate cover items. When the two were under a common cover item, they were at opposite ends. In nature, the two species probably avoid each other. Size possibly enforces interspecific avoidance.

Niche Separation

Hutchinson's (1965) definition of a niche is perhaps the most accurate of a poorly understood concept. "The intensive definition required may be obtained by considering a hyperspace every coordinate (x_1, x_2, x_3 ...) of which corresponds to a relevant variable in the life of a species of organism. A hypervolume can therefore be constructed, every point of which corresponds to a set of values of variables permitting the organism to exist." His *n*th dimensional, abstractly inhabited hypervolume can exist in two forms. The more theoretical, the fundamental niche, exists when no competitors are present. The second, the status most often achieved in nature, is the realized niche and occurs when organisms are in competition for limited resources (food, shelter, radiation, nesting sites, etc.).

The tendency for competition to bring about an ecological separation of closely related species is known as the competitive exclusion principle (Hardin, 1960). More commonly called Gause's Principle, the theory states that when communities are in equilibrium no two species occupy the same niche.

Lack (1944) stated that when two closely related species come into contact, interspecific competition forces them to one of the following states: (1) one species will eliminate the other, (2) the two may occupy allopatric, but often contiguous, geographic regions, (3) they may live in sympatry but occupy different habitats, (4) they may occupy the same habitat but differ in resource utilization. All of Lack's (1944) postulates can be considered variables of the competitive exclusion principle. Postulates three and four describe methods by which closely related species coexist.

This study has revealed several ways that *Coleonyx brevis* - *Coleonyx reticulatus* niche separation occurs. Laboratory behavioral data has shown that *C. reticulatus* is, at least partially, arboreal. Specimens were observed climbing frequently and, on two occasions, each escaped in a manner characteristic only of species with a well-developed climbing ability. Gross tail structure suggests different strategies of tail use in each species. Tails of _C. reticulatus_ are rather thin and elongate and do not appear to be used for fat storage to the extent that they are in _C. brevis_. Conversely, in _C. brevis_, tails are short and stubby and are obviously more steatocaudic. It follows that if _C. reticulatus_ utilizes the tail for climbing then the species would be less likely to autotomize the tail on predator encounter. If _C. reticulatus_ is partially arboreal, the species would be exposed to different prey than _C. brevis_, which would aid in reducing competition.

Data on the thermal ecology of the two is perhaps most revealing. Interspecific differences in temperature preferences in the laboratory thermal gradient were significant with _C. brevis_ preferring temperatures considerably warmer than _C. reticulatus_. Laboratory data are supported by field temperature data revealing that _C. brevis_ were more common during early, warmer hours at night. With a decrease in temperatures around 2200 hours, _C. brevis_ were less active and fewer were collected. Conversely, _C. reticulatus_ were active only at cooler temperatures brought by rains.

Such a difference in temperature preferences may be an indication of differences in the "time niche" of the two species (see Pianka, 1969). Air, substrate, and body temperatures are time dependent and therefore, a lizard's daily activities are geared directly to its thermoregulatory requirements. Hence, differences in preferred body temperatures between two species will produce differences in time of activity, the most activity occurring when a species can operate at its preferred temperature. Differences in activity periods expose species to different prey, thereby reducing competition for food (Pianka, 1969). It is suggested that C. reticulatus is more stenothermic and is active only during cooler temperatures, while C. brevis is rather eurythermic, active mainly during warmer temperatures and partially during cooler temperatures. Such differences in the "time niche" of the two aid in reducing competition.

Schoener and Gorman (1968) have shown how differences in prey size enable closely related species to coexist. In their study, two sympatric species were of quite different size. However, specimens of the two with similar snout-vent lengths took contrasting prey sizes. Though there are too few data on the food of C. reticulatus to form definite conclusions, the same situation may be occurring between the two Coleonyx. Schoener and Gorman (1968) demonstrated how the more aggressive nature of the male of a species might aid in overcoming larger prey. Likewise, the more aggressive nature of C. reticulatus may enable juveniles of the species to capture larger prey than adult C. brevis of similar size.

Grant (1972) defined character displacement as the process by which a character of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively. Huey and Pianka (1974) presented data revealing ecological character displacement in sympatric species of the lizard genus Typhosaurus in Africa. In their study, the range of a smaller species was shown to be included within the range of a larger species. Character displacement occurred in snout-vent lengths and head proportions, thereby reducing competition.

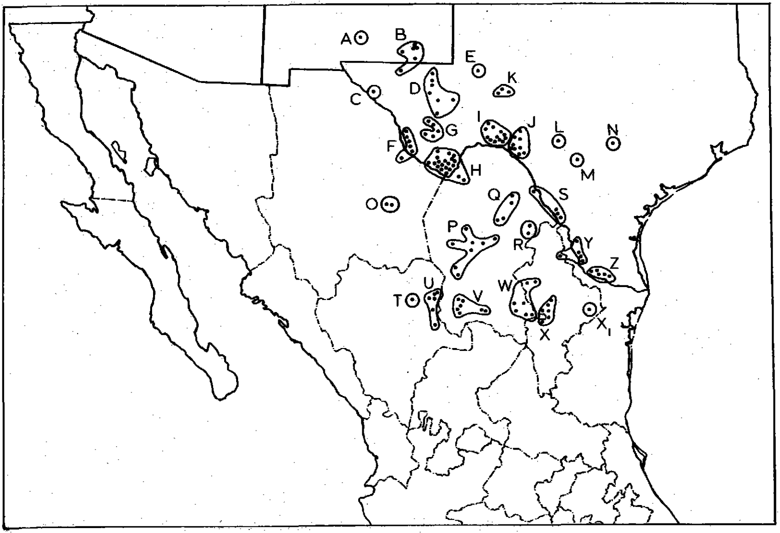
A similar situation may be occurring in C. brevis and C. reticulatus. Data on C. brevis in sympatry with C. reticulatus and C. brevis from localities where C. reticulatus is not known, show that selection may be favoring greater differences in snout-vent lengths between the two species under sympatric conditions. Of 30 C. brevis from Brewster County, Texas (occurring sympatrically with C. reticulatus), mean snout-vent length was 49.1 mm. Of 54 C. brevis from Val Verde County, Texas (not occurring sympatrically with C. reticulatus), mean snout-vent length was 51.3 mm. A t test showed the differences to be significant at the 0.01 level (t = 3.35, 120 d.f.). Selection may increase the size difference between the two under sympatric conditions, thereby reducing competition for food.

SYSTEMATICS

For statistical analysis, samples of Coleonyx brevis were pooled as shown in Figure 25. Designations for each of the pooled samples are listed below.

Pooled samples: A, Alamo Mountain, Otero County, New Mexico; B, Eddy County, New Mexico, and Culberson County, Texas; C, Hudspeth County, Texas; D, Loving, Reeves, and Pecos counties, Texas; E, Ector County, Texas; F, Presidio County, Texas, and northeastern Chihuahua, Mexico; G, Davis Mountains, Jeff Davis, Presidio, Brewster counties, Texas; H, Big Bend, Brewster County, Texas and northwestern Coahuila, Mexico; I, west of Pecos River, Terrell and Val Verde counties, Texas; J, east of Pecos River, Val Verde and Crockett counties, Texas; K, Reagan County, Texas; L, Edwards County, Texas; M, Uvalde County, Texas; N, Bexar County, Texas; O, near Ciudad Delicias and Camargo, Chihuahua, Mexico; P, central and western Coahuila, Mexico; Q, near Nueva Rosita, Coahuila, Mexico; R, Don Martin Dam, Coahuila, Mexico; S, near Nava, Coahuila, Mexico and Webb County, Texas; T, near Rodeo, Durango, Mexico; U, near Gomez Palacio and Cuencame, Durango, Mexico; V, near San Pedro and Parras, Coahuila, Mexico; W, Sierra Madre Oriental, near Soledad, Villaldama, and Santa Catarina, Nuevo Leon, Mexico, and near Santa Cruz, Coahuila, Mexico; X, near Monterrey, Garcia, Cienega de Flores, and Sabinas Hidalgo,

Figure 25. Sample localities of Coleonyx brevis from New Mexico, Texas, and Mexico. Black dots are records of Coleonyx brevis. Those records enclosed within a black line were pooled for statistical treatment. The letter associated with each pooled sample is the sample designation for those specimens and corresponds to the same letter used in the text.


A
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X1

Nuevo Leon, Mexico, and near Villa Garcia, Coahuila, Mexico; X_1, near General Bravo, Nuevo Leon, Mexico; Y, northeast of Sabinas Hidalgo, Nuevo Leon, Mexico, and near Zapata, Zapata County, Texas; Z, near Falcon Dam, Zapata County, Texas, near Rama, Rio Grande City, and Sullivan City, Starr County, Texas, and near La Joya, Hidalgo County, Texas.

Few specimens of *Coleonyx reticulatus* exist in museums. Therefore, data taken from those specimens are included in tabular form only (Table 12).

Non-geographic Variation

Before data on geographic variation can be analyzed, any non-geographic variation must be documented. No data were taken on ontogenetic variation. However, secondary sexual variation was studied in 36 specimens from Black Gap Wildlife Management Area, Brewster County, Texas (Table 13). Only one character (granules eye to eye) shows a significant difference between sexes. Because secondary sexual differences are not significant in other characters, the sexes have been considered together for geographic analysis.

Coefficients of variation are presented in Table 13. Only one character (presence of granules between supranasals) has a high coefficient of variation, due to the extremeness of the character state (present or absent). None of the other characters has a

Table 12. Squamative data from 15 specimens of *Coleonyx reticulatus*.

Museum	Number	Sex	SVL	INTNAS	SUPNAS	RPNAS/LPNAS	SUPLB	INFLB	PMENT	BRIL
TCWC	12855	F	84	6	2	5/5	6	5	9	51
TCWC	39330	M	84	6	1	6/6	6	6	11	57
TCWC	39331	F	89	7	1	6/6	6	5	11	54
TCWC	39332	F	82	6	1	6/6	6	6	9	57
TCWC	39333	M	71	6	1	6/6	6	6	9	55
TCWC	39334	M	79	6	0	6/6	5	6	9	52
BBNP	4262	F	84	7	1	6/5	6	5	11	55
DMNH	882	F	59	5	1	5/5	5	5	11	52
DMNH	794	F	89	7	2	5/5	6	7	10	50
DMNH	1157	F	83	7	1	5/5	7	6	10	61
DMNH	1158	F	84	6	1	5/5	5	4	10	50
DMNH	970	F	81	6	1	5/5	6	6	10	56
LACM	93432	Juv.	44	5	2	5/4	5	5	10	48
LACM	101266	M	76	6	1	6/6	6	7	11	60
RGW	5396	F	72	6	2	4/4	–	–	8	--

Table 12. (continued)

Museum	Number	GETE	PREOC	SAB	PREANP	SBPP	FTL	VSRS	DSRS	TUBROW
TCWC	12855	71	23	174	--	-	30	89	96	13
TCWC	39330	63	22	177	20	0	26	94	88	14
TCWC	39331	63	24	175	--	-	24	88	94	14
TCWC	39332	64	22	169	--	-	25	92	85	14
TCWC	39333	61	24	170	--	-	26	95	80	14
TCWC	39334	59	22	171	18	-	23	82	84	15
BBNP	4262	63	20	191	--	-	23	96	85	14
DMNH	882	65	20	170	20	0	27	95	89	14
DMNH	794	--	23	185	--	-	27	100	92	14
DMNH	1157	69	21	---	--	-	25	--	82	14
DMNH	1158	66	24	183	--	-	28	74	108	16
DMNH	970	64	26	193	--	-	26	98	89	16
LACM	93432	61	20	167	--	-	27	--	--	14
LACM	101266	57	23	170	20	0	24	92	80	14
RGW	5396	--	--	176	--	-	25	--	--	--

Table 13. Secondary sexual variation and coefficients of variation in a sample of *Coleonyx brevis* from Black Gap Wildlife Management Area, Brewster Co., Texas. F-values that are significant ($p \leq 0.05$) are indicated by an asterisk. Coefficients of variation are calculated for males and females together.

	Males			Females				
Character	N	Mean	SD	N	Mean	SD	F-Value	CV
INTNAS	25	4.12	0.67	13	4.15	0.55	0.043	15.46
SUPNAS	25	0.32	0.48	13	0.62	0.51	2.355	120.53
RPNAS	25	3.12	0.44	13	3.08	0.28	0.069	12.82
LPNAS	25	3.12	0.44	13	3.15	0.38	0.098	13.54
SUPLB	26	5.31	0.55	13	5.62	0.51	3.732	9.82
INFLB	26	4.88	0.65	13	4.92	0.49	0.022	12.54
PMENT	26	6.27	0.87	13	6.69	0.63	1.963	12.71
BRIL	25	39.68	2.30	13	41.00	3.08	0.943	6.02
GETE	25	40.80	2.48	13	43.23	3.17	6.830*	6.63
PREOC	25	13.84	1.25	13	14.62	1.12	3.728	8.64
SAB	25	115.92	5.11	13	114.00	4.67	2.125	4.25
FTL	26	15.04	1.04	13	15.46	1.05	1.576	6.94

coefficient of variation high enough to exclude it from analysis of geographic variation.

Geographic Variation

The geographic variation in morphology is described in the following section with reference to the pooled samples illustrated in Figure 25, p. 131. Frequently, pooled samples that occur in recognized biotic areas (i.e., Trans-Pecos Region, Mexican Plateau) may be discussed collectively in relation to other areas.

Number of internasal scales. The scales separating the most dorsal postnasals are internasals. In eublepharine lizards such scales are granular in size and shape and border the most dorsal postnasals medially and the supernasals posteriorly (Fig. 2, p. 15).

In *C. brevis* individual variation is from three to five. However, little significant variation occurs throughout the range. Geographic variation in this character in pooled samples is listed in Table 14 and slight trends are noted. Specimens from the Trans-Pecos area of Texas and New Mexico (areas ABCDFGH) tend to have slightly more internasals ($\bar{x} = 4.4$) than do specimens from the Gulf Coastal Plains along the Rio Grande of Mexico and southern Texas (areas QRSYZ; $\bar{x} = 3.8$). Likewise, a sample of 25 specimens from Reagan County, Texas (area K) has a mean of 4.3, whereas

Table 14. Geographic variation in four squamative characters of *Coleonyx brevis* (INTNAS, SUPNAS, RPNAS, LPNAS). Areas A-Z are illustrated in Fig. 25, p. 131. Sample sizes are followed by means, standard deviations, and ranges.

	INTNAS			SUPNAS			RPNAS			LPNAS		
Area	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range
A	4	4.5±0.6	4-5	4	0.5±0.6	0-1	4	3.0±0	3	4	3.2±5	3-4
B	18	4.4±0.5	4-5	18	0.9±0.2	0-1	18	3.1±0.4	3-4	18	3.3±0.8	1-5
C	1	5.0	---	1	0	---	1	3.0	---	1	3.0	---
D	11	3.9±0.7	3-5	11	0.3±0.5	0-1	11	3.3±0.5	3-4	11	3.3±0.5	3-4
E	1	4.0	---	1	0	---	1	---	---	1	---	---
F	9	4.3±0.7	3-5	9	0.2±0.4	0-1	9	3.0±0	3	9	3.0±0	3
G	6	4.0±0.6	3-5	6	0.5±0.5	0-1	6	3.4±0.5	3-4	6	3.4±0.5	3-4
H	97	4.0±0.6	3-5	97	0.3±0.4	0-1	97	3.1±0.4	2-4	97	3.1±0.4	2-4
I	54	4.1±0.6	3-5	54	0.4±0.5	0-1	54	3.2±0.4	3-4	54	3.1±0.4	3-4
J	14	4.1±0.6	3-5	14	0.4±0.5	0-1	14	3.2±0.4	3-4	14	3.3±0.6	2-4
K	25	4.3±0.6	3-5	25	0.3±0.5	0-2	25	3.0±0.2	3-4	25	3.1±0.2	3-4
L	1	4.0	4	1	1.0	1	1	5.0	5	1	5.0	5
M	2	3.5±0.7	3-4	2	0	---	2	3.0±0	3	2	3.0±0	3
N	2	3.5±0.7	3-4	2	0.5±0.7	0-1	2	3.0±0	3	2	3.5±0.7	3-4
O	1	5.0	5	1	0	---	1	4.0	4	1	4.0	4
P	9	3.9±0.7	3-5	9	0	---	9	3.3±0.5	3-4	9	3.3±0.5	3-5
Q	7	3.6±0.5	3-5	7	0.1±0.3	0-2	7	3.3±0.5	3-5	7	3.3±0.5	3-5
R	10	3.9±0.7	3-5	10	0.3±0.6	0-2	10	3.8±0.7	3-5	10	3.8±0.9	3-5
S	28	4.0±0.8	3-6	28	0.1±0.4	0-1	28	3.7±0.6	3-5	28	3.8±0.5	3-5
T	4	4.3±0.9	3-5	4	0.5±0.5	0-1	4	2.7±0.5	2-3	4	3.0±0	3
U	16	4.2±0.7	3-5	16	0.5±0.5	0-1	16	3.8±0.4	3-5	16	3.8±0.5	3-5
V	9	4.4±0.8	3-6	9	0.3±0.5	0-1	9	3.3±0.5	3-4	9	3.3±0.5	3-4
W	19	3.9±1.2	3-5	19	0.4±0.5	0-1	19	3.5±0.5	3-4	19	3.4±0.5	3-4
X	7	4.4±0.5	4-5	7	0.4±0.5	0-1	7	3.7±0.7	3-5	7	3.7±0.7	3-5
X_1	1	6.0	---	1	1.0	---	1	4.0	---	1	4.0	---
Y	21	3.8±0.6	3-5	21	0.3±0.5	0-2	21	4.0±0.4	3-5	21	4.0±0.4	3-5
Z	30	3.6±0.5	2-4	30	0.2±0.5	0-2	30	3.9±0.7	3-6	30	3.9±0.4	3-5

specimens from the Edwards Plateau average 3.7.

Specimens from the Mesa del Norte of Mexico (areas PTUV; $\bar{x}$ = 4.2) have a mean similar to the Trans-Pecos specimens. One specimen from near Ciudad Deliacias, Chihuahua, has five internasals and one from eastern Nuevo Leon has six. However, the sample size is too small to permit meaningful conclusions to be drawn regarding those specimens. Samples from the Saltillo-Monterrey area of the Sierra Madre Oriental have a slightly lower mean (areas WX; $\bar{x}$ = 4.1).

Geographic variation is in the form of slight north-south and west-east clines. Generally, the highest phenotypes occur in more northern and western populations while geographically intermediate populations represent slightly lower phenotypes. The most southeastern populations are represented by the lowest phenotypes.

Presence of granules between supranasals. Occasionally, a granule scale separates the supranasals medially (Fig. 2, p. 15). Geographic variation in this character in pooled samples is given in Table 14, p. 137, and the overall frequency of the granule was 36% (N = 392). Specimens from Otero and Eddy counties, New Mexico, and Culberson County, Texas, average highest (areas AB; $\bar{x}$ = 0.72) while to the south, specimens from areas CDFGH average very low ($\bar{x}$ = 0.26). A gradual increase occurs to the east; specimens from areas IJ average 0.4 and areas LMN average 0.5. As in numbers on internasals, areas RSYZ compose a complex of similar phenotypes

($\bar{x} = 0.2$). Specimens from localities extending across the southern border of the Mesa del Norte (TUVWX) average 0.4 and specimens from the central part of the Mesa del Norte (P) and from near Camargo, Chihuahua, (O), had no granules between supranasals.

No distinct pattern in geographic variation in this character is noted; specimens from geographical proximate localities in the northwest have both high and low percentages of frequency of the scale. Likewise, specimens from localities in the east and southeast show similar percentages.

Number of right and left postnasals. All scales bordering the nostril on the dorsal, posterior, and ventral sides, exclusive of the supranasals, are postnasals (Fig. 2, p. 15). Generally, postnasals are larger than granules, spheroid or ellipsoid in shape, and quite distinct from the reniform supranasals. Numbers of right and left postnasals of sample means were nearly identical, the greatest difference being 0.3 of a postnasal. Therefore, to facilitate the handling of data, in most cases the sample means of right and left postnasals were averaged and the results studied for variation (Table 14, p. 137).

Specimens from localities in New Mexico and Trans-Pecos, Texas, (ABCDFGHIJ), have a mean of 3.2. To the east and south means increase; Edwards Plateau samples (LMN) average 3.7 and the Gulf Coastal Plain specimens (RSYZ) average 3.8. Specimens from the Sierra Madre Oriental area and the southern border of the Mesa del Norte average 3.6.

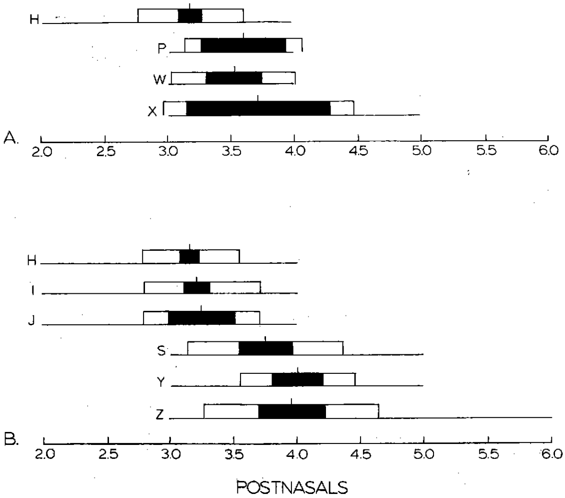
North-south clinal variation in number of right postnasals is displayed from Trans-Pecos Texas south into southern Coahuila, and from Trans-Pecos Texas south through the Rio Grande drainage to the Rio Grande Valley (Fig. 26, A and B).

Variation within this character reveals that populations tend to fall into three groups: Trans-Pecos Texas and New Mexico, the Rio Grande Valley, and the Mesa del Norte. Smallest values occur in specimens from the Trans-Pecos Region, medial values are characteristic of specimens from the Mesa del Norte area, and highest values are found in specimens from the Rio Grande Valley. Specimens with intermediate values occur between the Rio Grande Valley, Trans-Pecos Region, and the Mesa del Norte areas suggesting that gene exchange probably occurs from the Rio Grande Valley to the west with the Mesa del Norte specimens, and to the north with the Trans-Pecos Region specimens.

Number of supralabials. Labials gradually decrease in size posteriad. Near the angle of the jaw, scales bordering the mouth frequently are granular and identical in appearance to other head scales. To aid in counting, labials were counted to the anterior margin of the eye. Admittedly, this reduces the actual labial count, but it does serve as a reference by which populations can be compared.

Supralabials vary randomly throughout the range of *C. brevis*

Figure 26. Geographic variation in number of postnasals in samples of Coleonyx brevis. Letters refer to pooled samples. Vertical line represents the mean; open rectangle, once the standard deviation; black rectangle, twice the standard error; horizontal line, the range of variation. (A) Trans-Pecos Texas to southeastern Coahuila. (B) Rio Grande drainage.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POSTNASALS

(Table 15). Specimens from west of the Pecos River (ABCDFGHI) average from 4.9 to 5.4, while means from the Gulf Coastal Plain complex (RSYZ) range from 4.8 to 5.7. The specimens from the Sierra Madre Oriental in southeastern Coahuila have means from 4.8 to 5.0 while specimens from the Mesa del Norte range from 5.0 to 5.5. Inconsistent variation present in this character prevents its use as a taxonomic aid.

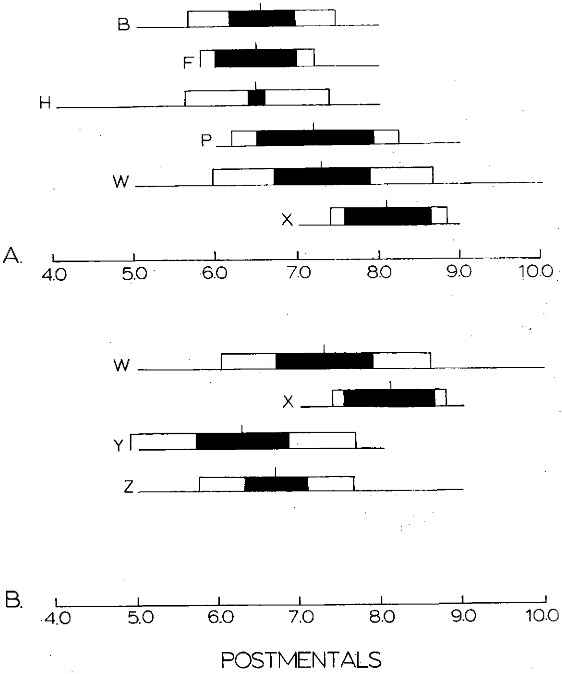
Number of infralabials. As in supralabials, infralabials were counted to the anterior margin of the eye. Most specimens have fewer infralabials than supralabials. The number of infralabials varies randomly throughout the range (Table 15). Specimens from west of the Pecos River (ABCDFGHI) have means from 4.4 to 5.1, while the Gulf Coastal Plain specimens (RSYZ) average from 4.6 to 5.3. Specimens from areas W and X (southeastern Coahuila and Nuevo Leon) have means of 5.1 and 4.3, respectively, while specimens from the Mesa del Norte average from 4.7 to 6.0. Inconsistent variation present in this character prevents its use as a taxonomic aid.

Number of postmentals. All granules bordering the mental posteriorally are postmentals. Among individuals of *C. brevis* the character is quite variable, ranging from four to ten and sample means show some geographic distinction (Table 15). Figure 27, A and B, illustrates the variation present among pooled samples.

Table 15. Geographic variation in four squamative characters of *Coleonyx brevis* (SUPLB, INFLB, PMENT, BRIL). Areas A-Z are illustrated in Fig. 25, p.131. Sample sizes are followed by means, standard deviations, and ranges.

	SUPLB			INFLB			PMENT			BRIL		
Area	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range
A	4	5.0	5	4	5.0	5	4	6.5±0.6	6-7	4	39.5±3.8	35-44
B	18	5.4±0.5	5-6	18	4.9±0.5	4-6	18	6.6±0.9	5-8	18	40.6±3.3	35-45
C	1	5.0	---	1	5.0	---	1	6.0	---	1	45.0	---
D	9	5.3±0.5	5-6	9	4.5±0.5	4-5	11	6.2±0.7	5-7	11	41.8±1.8	39-45
E	1	6.0	---	1	4.0	---	1	8.0	---	1	43.0	---
F	9	5.2±0.4	5-6	9	5.1±0.6	4-6	9	6.5±0.7	6-8	9	39.5±2.0	36-42
G	7	5.3±0.7	4-6	7	4.8±0.7	4-6	6	6.7±1.4	5-9	6	39.6±2.5	35-42
H	99	5.3±0.6	4-7	99	5.0±0.6	4-6	97	6.5±0.8	4-8	97	40.1±2.3	34-46
I	53	4.9±0.6	4-6	53	4.4±0.5	4-6	54	5.9±0.8	4-8	54	40.0±2.0	35-44
J	12	5.1±0.7	4-6	12	4.5±0.5	4-5	14	6.3±1.1	5-9	14	39.8±1.6	37-42
K	23	5.2±0.5	4-6	23	4.7±0.4	4-5	25	6.0±0.8	5-7	25	39.6±2.0	37-45
L	--	---	---	--	---	---	1	6.0	6	--	---	---
M	--	---	---	--	---	---	2	6.5±0.7	6-7	--	---	---
N	--	---	---	--	---	---	2	6.0	6	--	---	---
O	1	5.0	5	1	6.0	6	2	7.5±0.7	7-8	2	39.0±1.4	38-40
P	9	5.2±0.8	5-7	9	4.7±0.4	4-5	9	7.2±1.1	6-9	9	41.6±3.5	38-46
Q	6	4.8±0.4	4-5	6	4.6±0.5	4-5	7	6.6±1.2	5-9	7	41.0±1.9	36-48
R	9	5.3±0.5	5-6	9	5.2±0.6	4-6	10	6.7±1.0	5-8	10	44.0±2.4	40-48
S	29	5.6±0.6	4-7	28	5.3±0.7	4-7	28	6.4±0.8	5-8	28	40.6±2.0	38-46
T	--	---	---	--	---	---	4	8.3±0.9	7-9	--	---	---
U	15	5.5±0.7	5-7	15	5.1±0.6	4-6	16	7.6±1.2	6-10	16	41.0±2.3	37-46
V	9	5.3±0.5	5-6	9	5.1±0.6	4-6	9	7.1±0.8	6-8	9	41.5±2.2	38-44
W	19	5.0±0.4	4-6	19	5.1±0.5	4-6	19	7.3±1.3	5-10	19	42.1±2.3	37-46
X	7	4.8±0.7	4-6	7	4.3±0.5	4-5	7	8.1±0.7	7-9	7	41.7±3.2	37-46
X_1	--	---	---	--	---	---	1	9.0	---	--	---	---
Y	19	5.7±0.6	5-7	19	5.1±0.7	4-6	21	6.3±1.4	6-8	21	42.4±3.1	36-46
Z	21	5.4±0.6	5-7	21	4.9±0.4	4-6	30	6.7±0.9	5-9	30	43.9±2.9	39-49

Figure 27. Geographic variation in number of postmentals in samples of Coleonyx brevis. (See Fig. 26, p. 142 for explanation of analysis.) (A) New Mexico to southern Mesa del Norte. (B) Mesa del Norte to Gulf Coastal Plain.


B
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9.0
10.0
POSTMENTALS

Figure 27A, representing a north-south transect drawn from New Mexico to the southern part of Mesa del Norte, reveals that specimens from the southern localities tend to have a higher number of postmentals than specimens from more northern localities. Figure 27B, illustrating variation among specimens from the Mesa del Norte and the Gulf Coastal Plain, shows that Rio Grande Valley specimens have slightly lower values for this character than do specimens from the Mesa del Norte. In general, specimens from the Mesa del Norte and the Sierra Madre Oriental have the most postmentals (TUVPWX; $\bar{x} = 7.6$) while the lowest numbers of postmentals occur in specimens from the Trans-Pecos Region (ABCDFGH; $\bar{x} = 6.3$) and the Rio Grande Valley (YZ; $\bar{x} = 6.5$).

On the basis of this character, specimens can be separated into two groups, one including specimens from the Trans-Pecos Region, the Rio Grande drainage, and the Rio Grande Valley, and one including specimens from the Mesa del Norte.

Number of extrabrillar fringe scales. All scales orbiting the eye were considered as extrabrillar fringe scales (Fig. 2, p. 15). Size and shape of the scales vary from short, blunt scales to elongate scales with curved, pointed tips. Overall range in number of the scale is from 34 to 49. Sample means of this character show some geographic distinction (Table 15, p. 144). No clinal variation occurs in the north-south transect drawn from Trans-Pecos Texas to southern Coahuila. However, distinct clinal variation is noted in samples occurring along the Rio Grande drainage (Fig. 28A). Specimens from the Trans-Pecos Region have a mean of 40.0 to 40.1, while localities from Webb County, Texas produce phenotypes that average 40.6. Specimens from the Rio Grande Valley have means of 42.4 and 43.9.

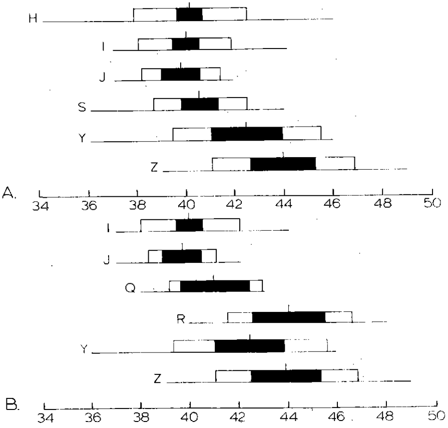
A transect drawn from the Pecos River area of Texas (IJ) south to area R and into the Rio Grande Valley (Fig. 28B) reveals that areas R and Q are quite distinct. Though area Q is geographically the closest to area R, similarities of area R are with areas Y and Z of the Rio Grande Valley. Areas Q, I, and J are similar.

Number of granules between eyes. The number of granules in a single row was counted between the center of the orbits and data on this scale are given in Table 16. Clinal variation is present in the north-south transect (Fig. 29A) and in the transect drawn along the Rio Grande drainage (Fig. 29B). In both, the more southern populations tend to be utilizing the higher values within the range of this character.

Of special interest is the variation observed when specimens from the Pecos River (IJ) are compared with specimens from eastern Coahuila (QR) (Fig. 29C). As in number of extrabrillar fringe scales, area Q, distinct from its most proximate locality, area R, has affinities with areas I and J.

Of additional interest is the general pattern expressed by increasing values of this character. The lowest values occur in

Figure 28. Geographic variation in extrabrillar fringe scales in samples of Coleonyx brevis. (See Fig. 26, p. 142 for explanation of analysis.) (A) Rio Grande drainage. (B) Pecos River, eastern Coahuila, to Rio Grande Valley.



EXTRABRILLAR FRINGE SCALES

Table 16. Geographic variation in three squamative characters of _Coleonyx brevis_ (GETE, PREOC, SAB). Areas A-Z are illustrated in Fig. 25, p.131. Sample sizes are followed by means, standard deviations, and ranges.

Area	GETE			PREOC			SAB		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
A	4	39.3±1.0	38-40	4	13.8±0.9	13-15	4	111.7±4.5	107-117
B	18	41.7±3.2	35-47	18	14.9±1.5	13-18	18	114.0±4.6	105-123
C	1	38.0	---	1	14.0	---	1	111.0	---
D	9	41.9±3.7	39-50	9	14.4±0.8	13-15	11	118.8±4.9	110-125
E	1	39.0	---	1	16.0	---	1	141.0	---
F	9	40.0±2.4	38-45	9	15.1±1.7	13-18	8	114.6±7.8	101-123
G	--	---	---	--	---	---	7	118.1±7.7	108-126
H	95	41.5±2.8	36-48	96	14.6±1.2	11-18	97	114.8±5.0	103-130
I	53	40.6±2.3	36-46	53	14.6±1.3	12-17	53	119.0±4.8	108-130
J	12	41.6±3.5	37-48	12	14.4±1.6	12-17	14	122.5±8.9	114-145
K	23	41.3±2.8	37-47	23	14.7±1.0	13-17	25	117.2±3.1	110-125
L	--	---	---	--	---	---	1	112.0	---
M	--	---	---	--	---	---	2	123.0±1.4	122-124
N	--	---	---	--	---	---	2	121.5±2.1	120-123
O	2	41.5±3.5	39-44	1	15.0	---	1	123.0	---
P	9	45.0±2.8	40-49	9	14.3±1.3	12-16	9	116.6±6.1	110-128
Q	6	40.6±2.7	38-44	6	15.3±.51	15-16	7	122.0±4.0	117-127
R	10	47.3±2.8	44-51	10	15.7±1.2	14-18	10	130.3±4.8	120-137
S	23	43.4±4.0	37-49	22	14.6±1.0	13-17	26	125.3±5.3	116-133
T	--	---	---	--	---	---	4	126.5±3.8	124-132
U	16	45.7±3.4	38-52	16	15.7±1.6	13-19	16	124.6±6.2	114-135
V	9	46.0±3.4	41-49	9	15.8±1.0	14-17	9	126.7±4.0	121-131
W	19	46.4±4.9	37-56	18	15.0±1.0	13-17	19	116.7±3.7	110-125
X	6	45.5±4.2	38-50	6	14.8±0.7	14-16	7	125.7±4.0	120-133
X_1	--	---	---	--	---	---	1	126.0	---
Y	19	42.8±3.0	36-46	19	14.6±1.2	13-17	21	131.3±5.9	122-141
Z	20	44.4±3.2	40-51	20	14.7±1.0	13-16	30	131.5±5.2	118-141

Figure 29. Geographic variation in number of granules eye to eye in samples of _Coleonyx brevis_. (See Fig. 26, p. 142 for explanation of analysis.) (A) New Mexico to southern Mesa del Norte. (B) Rio Grande drainage.

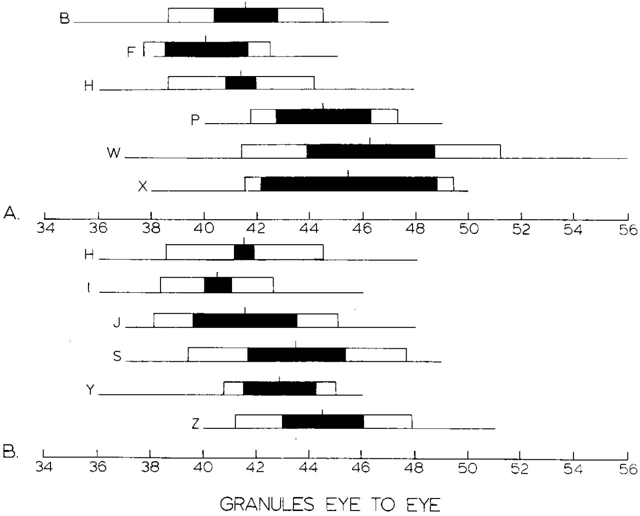
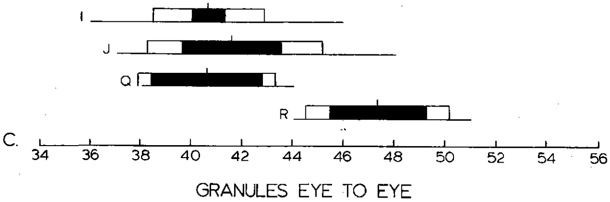

B
F
H
P
W
X
A.
34
36
38
40
42
44
46
48
50
52
54
56
H
I
J
S
Y
Z
B.
34
36
38
40
42
44
46
48
50
52
54
56
GRANULES EYE TO EYE

Figure 29. (continued) (C) Pecos River to eastern Coahuila.


I
J
Q
R
C.
34
36
38
40
42
44
46
48
50
52
54
56
GRANULES EYE TO EYE

Trans-Pecos Texas, values become larger in specimens from the Rio Grande drainage to the Rio Grande Valley, while values increase to the west. Rio Grande Valley specimens show association with specimens from the Sierra Madre Oriental. Mesa del Norte and Sierra Madre Oriental specimens seem to form a homologous unit.

Number of preoculars. The number of granules in a single row (preoculars) was counted from the anterior margin of the eye to the medial postnasal. Variation of means of samples with seven or more specimens was minimal (range = 14.3 to 15.8, Table 16). Specimens from the Trans-Pecos Region tend to form a group of similar phenotypes. Likewise, samples from the Mesa del Norte, with the exception of area P, tend to group together, having slightly higher means than samples from other areas.

Number of longitudinal scale rows around body. The number of longitudinal scale rows around body, including dorsal and ventral scales, was counted at midbody. Small differences in the position of counting (three or four scale rows anteriad or posteriad) resulted in less than three percent variation in number of scale rows around body. Geographically, this character is quite variable and is perhaps the best character for indicating population distinction in *C. brevis* (Table 16). Overall sample mean variation was from 101 to 145 and distinct clinal variation can be observed by analyzing data presented in Figure 30. In the north-south transect (Fig. 30A), the southwestern Coahuila samples (UV) average higher than samples from central Coahuila, Trans-Pecos Texas, and New Mexico. Specimens from areas UV are quite distinct from P, the most proximate locality.

The transect drawn along the Rio Grande drainage (Fig. 30B), illustrating distinct northwest-southeast clinal variation, indicates that samples from near the Pecos River (IJ) are distinct from the Big Bend sample (H), while the Webb County, Texas sample (S) is similar to the sample from east of the Pecos River (J). The Rio Grande Valley samples (YZ) are most distinct, with the character state averaging highest. A comparison of specimens from the Pecos River area of Texas (IJ) to specimens from eastern Coahuila (QR) (Fig. 30C) shows that areas I, J, and Q fall into a phenotypically similar complex, while areas R, Y, and Z do likewise.

The pattern expressed in this character seems to consist of three major groups. Specimens from Durango, Chihuahua, and southwestern Coahuila form one homologous unit of high values. Specimens from the Rio Grande Valley, likewise, are represented by high values. Intermediate between the two regions is a projection of specimens with low values, extending southeastward from Trans-Pecos Texas into central and southeastern Coahuila. The extension of specimens separates the two areas of specimens with high values (southwestern Coahuila and the Rio Grande Valley). There may be gene exchange between specimens from the projection and the Rio

Figure 30. Geographic variation in number of longitudinal scale rows around body in samples of Coleonyx brevis (non-grouped). (See Fig. 26, p.142 for explanation of analysis.) (A) New Mexico to southern Mesa del Norte. (B) Rio Grande drainage.

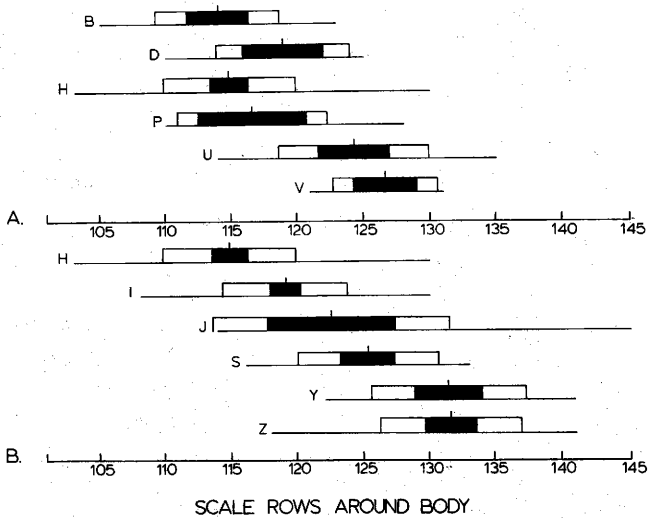
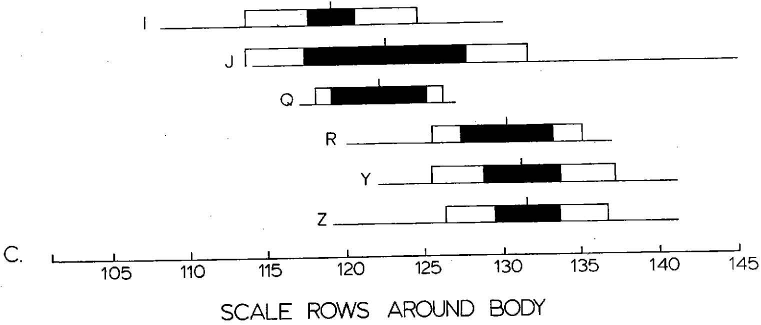

B
D
H
P
U
V
A.
105
110
115
120
125
130
135
140
145
H
I
J
S
Y
Z
B.
105
110
115
120
125
130
135
140
145
SCALE ROWS AROUND BODY

Figure 30. (continued) (C) Pecos River, eastern Coahuila, to Rio Grande Valley.


I
J
Q
R
Y
Z
C.
105
110
115
120
125
130
135
140
145
SCALE ROWS AROUND BODY

Grande Valley, as intermediate values are found in specimens from geographically intermediate areas.

By grouping and comparing areas from each region across the southern limits of the range, the variation expressed in this character can be visualized (Fig. 31). Grouped areas are U-V (Durango and southwestern Coahuila), P-W (central and southeastern Coahuila), and Y-Z (Rio Grande Valley). Areas P and W, the southward extension of similar phenotypes extending from Trans-Pecos Texas, separate the two areas (U, V and Y, Z) of higher values.

Number of preanal pores. Only fully developed preanal pores in males were counted. Frequently, females possess enlarged preanal scales with slight indentations. However, those are not accurate indications of preanal pores. Except for two samples of small size, overall variation in sample means was small. (Range = 4.0 to 5.0; Table 17) and no geographic distinction in this character was noted. Data suggest that ontogenetic variation occurs in the development of prenal pores rendering the character useless taxonomically.

Number of scales between preanal pores. In males, the total number of scales between preanal pores was counted. Samples from the southeastern part of the range tend to have a slightly higher mean (Table 17). However, concurrent with the number of preanal pores, this character appears to vary ontogenetically and is useless

Figure 31. Geographic variation in number of longitudinal scale rows around body in samples of Coleonyx brevis (grouped). (See Fig. 26, p.142 for explanation of analysis.) Grouped pooled samples from northeastern Durango and southwestern Coahuila, southeastern Coahuila, and Rio Grande Valley.

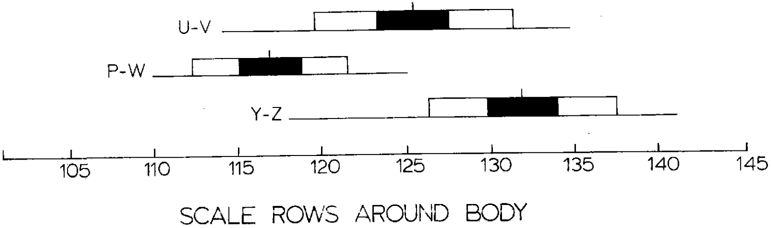

U-V
P-W
Y-Z
105
110
115
120
125
130
135
140
145
SCALE ROWS AROUND BODY

Table 17. Geographic variation in three squamative characters of *Coleonyx brevis* (PAP, SBPAP, FTL). Areas A-Z are illustrated in Fig. 25, p.131. Sample sizes are followed by means, standard deviations, and ranges.

Area	PAP			SBPAP			FTL		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
A	3	4.6±0.57	4-5	3	1.3±0.57	1-2	4	15.0±0	15
B	8	4.0±0	4	8	1.2±0.46	1-2	18	15.0±0.9	13-16
C	0	---	---	0	---	---	1	15.0±0	15
D	6	4.6±1.0	4-6	6	2.0±0.63	1-3	11	14.7±1.1	13-17
E	1	5.0±0	5	1	1.0±0	1	1	15.0±0	15
F	2	4.0±0	4	2	2.5±0.7	2-3	9	15.2±0.9	14-17
G	6	4.0±0	4	6	1.5±0.5	1-2	6	15.5±1.2	14-17
H	48	4.0±0.2	4-5	48	1.9±0.6	1-4	97	15.1±1.2	13-22
I	32	4.1±0.3	4-5	32	1.4±0.5	1-3	53	13.7±1.0	11-16
J	12	4.2±0.6	4-6	12	1.4±0.7	0-3	13	14.6±1.0	13-16
K	17	4.4±0.7	4-6	17	1.5±0.5	1-2	25	14.0±0.8	12-15
L	1	4.0±0	4	1	1±0	1	1	15.0±0	15
M	1	4.0±0	4	1	1±0	1	2	15.5±0.7	15-16
N	1	4.0±0	4	1	1±0	1	2	15.0±1.4	14-16
O	1	4.0±0	4	1	3.0±0	3	2	14.0±0	14
P	5	4.0±0	4	5	2.0±0	2	9	16.0±1.0	15-18
Q	2	4.0±0	4	2	3.5±0.7	3-4	6	14.3±1.0	13-16
R	6	4.0±0	4	6	3.0±1.0	2-5	9	14.3±0.7	13-15
S	14	4.1±0.8	4-6	14	2.2±0.7	1-4	27	14.4±1.1	13-17
T	2	2.5±0.7	2-3	2	3.5±0.7	3-4	4	14.5±1.0	14-16
U	5	4.2±0.4	4-5	5	2.2±1.4	2-4	16	15.8±1.2	14-18
V	3	3.3±1.5	2-4	3	1.6±0.5	1-2	9	17.0±1.2	16-19
W	8	4.5±1.0	4-6	8	2.6±1.0	2-5	19	15.3±0.7	14-17
X	3	4.0±0	4	3	3.3±1.1	2-4	7	14.5±1.1	13-16
X_1	0	---	--	0	---	---	1	16.0±0	16
Y	4	4.0±0	4	4	3.0±0	3	6	15.1±0.8	14-17
Z	13	4.2±0.5	4-6	13	3.1±0.8	1-4	21	15.5±0.8	14-17

as an indication of genetic affinity.

Number of fourth toe lamellae. In individuals, the number of fourth toe lamellae was found to be quite variable, ranging from 11 to 17; however, variation in sample means was not as extreme (Table 17). Data on means reflect some geographic distinction with specimens from the Trans-Pecos Region possessing the fewest number of lamellae and those from the Rio Grande Valley and the Mesa del Norte having slightly higher values.

Discussion

In the analysis of univariate statistics of the data, trends with respect to geographic variation within the species were noted. Conclusions are based on variation exhibited by samples of at least seven specimens; placing emphasis on samples of smaller size has been avoided.

Possible routes of gene exchange among populations were considered, and clinal variation within the species has been documented. Samples represented in the following transects were compared: 1) southern New Mexico, Trans-Pecos Texas, central Coahuila, southeastern Coahuila, 2) Rio Grande drainage (Big Bend, mouth of Pecos River, Webb County, Rio Grande Valley). In one character, specimens in a transect from Trans-Pecos Texas through central Coahuila to southwestern Coahuila and Durange were compared. In several situations, particular samples were compared in areas where more differentiation seemed to be occurring.

Geographic variation in C. brevis tends to be on a north-south basis, with five characters exhibiting geographic variation in this form (postnasals, postmentals, extrabrillar fringe scales, granules eye to eye, and scale rows around body). In those characters highest values are found in the southern populations.

The first north-south transect (New Mexico-southeastern Coahuila) shows slight clines in the following characters: postnasals and extrabrillar fringe scales. The clines are more defined in the following characters: postmentals, granules eye to eye, and scale rows around body. Two characters (postmentals and granules eye to eye) show slight clines in the second north-south transect (Rio Grande drainage) and strongly defined clines are exhibited by the following characters: postnasals, extrabrillar fringe scales, and scale rows around body.

An interesting relationship exists among specimens from the Pecos River area of Texas (IJ) and eastern Coahuila (QR). Data reveal a strong break between two geographically proximate areas (Q and R). In three characters (granules eye to eye, extrabrillar fringe scales, scale rows around body), area Q shows strong affinities with areas I and J to the north. In the same characters, areas P and Q, geographically the closest to R, are quite unlike R. R is phenotypically similar to specimens from the Rio Grande Valley (Y and Z) to the south.

This relationship corresponds with vegetational patterns of the area. Localities represented by Q (near Villa Union, Coahuila) are characteristically grassland with intermediate areas of limestone outcropping, much as is found in areas I and J (Val Verde and Terrell counties, Texas). Area R (around Don Martin Dam, Coahuila) has quite different vegetation, consisting of brushland and scrub desert as is found throughout south Texas, from Laredo to the Rio Grande Valley. Possibly the differences in vegetation types have served in restricting gene flow between the two areas; thus, strong character differences have occurred.

Generally, overall variation reveals that the species separates into three major geographic groups. All specimens from Trans-Pecos Texas and New Mexico are quite similar and represent one group. Specimens from Webb County and the Rio Grande Valley tend to form the second group. Specimens from the Mesa del Norte, west of the Sierra Madre Oriental (Coahuila, Durango, and Chihuahua), form the third group. Slight variations within this framework occur.

In three characters (granules eye to eye, postnasals, and fourth toe lamellae) specimens tend to fall into the three major groupings. Geographic intermediate populations are represented by intermediate values. One character (postmentals) suggests a combination of two major groups (Trans-Pecos Region, Rio Grande Valley and Mesa del Norte). Another character (scale rows around body) suggests another combination. In this character specimens from southwestern Coahuila and Durango separate into one group, Rio Grande Valley specimens into another, and the third group is formed by the Trans-Pecos region with a projection extending to southeastern Coahuila. Specimens with intermediate values are found in geographically intermediate areas, between the Rio Grande Valley localities and the extension from Trans-Pecos Texas (to southeastern Coahuila), suggesting gene exchange between the two regions. The region of southwestern Coahuila and northeastern Durango has been shown to be a particularly active area of speciation in several groups of reptiles. The area, referred to as the Bolson de Mapimi, has two endemic species of Uma (Schmidt and Bogert, 1947; Williams and Smith, 1959), a distinct subspecies of Arizona elegans (Klauber, 1946) and an endemic species of Gopherus (Legler, 1959). Indeed, the area is quite unique with respect to evolutionary activity and it is not surprising to find that C. brevis from the area tend to form a homologous unit, divergent from contiguous populations to the east. Interestingly, in the most reliable character (scale rows around body) no intermediate values are found in specimens immediately to the east, indicating at least restricted gene exchange between the two regions.

In recent years, minimal geographic variation within a species has been subject to several interpretations. Ideally, variation in morphology is an expression of the genetic construction within a species. However, Fox (1948) and Fox et al., (1961) have demonstrated in laboratory experiments on snakes that temperature and humidity may have a significant effect on the variation of some squamative characters. That minimal geographic variation in natural populations is exclusively the result of environmental conditions has not been proven.

Multivariate Analysis

Analysis of variance.

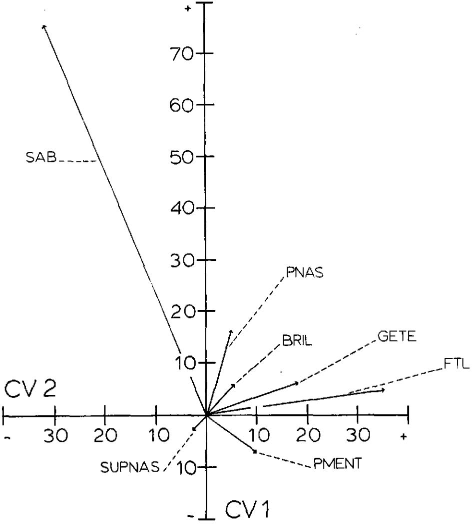
To assess variational trends with multiple characters considered simultaneously, the data were subjected to a multivariate analysis of variation. Seven characters were used; seven samples were omitted due to insufficient data. Multivariate analysis of variance (MANOVA) maximizes the influence of characters that differ among populations and minimizes character variation that approaches intrapopulational variation. Considering multiple characters simultaneously, MANOVA illustrates geographic variation more completely than do conventional univariate techniques.

Data on vector coefficients, percent influence, and median values for each character are given in Table 18. The first two canonical variates account for the greatest percent of total variation within the species (I = 54.36%, II = 25.43%). A vector diagram (Fig. 32) illustrates the percent influence of each

Table 18. Vector coefficients and their percent influence for the first two canonical variates, and median values for each character. Characters are: number of longitudinal scale rows (SAB), number of supranasals (SUPNAS), number of postnasals (PNAS), number of postmentals (PMENT), number of extrabrillar fringe scales (BRIL), number of fourth toe lamellae (FTL), and number of granules eye to eye (GETE).

	Canonical Variate I		Canonical Variate II		
Character	Vector Coefficient	% Influence	Vector Coefficient	% Influence	Median
SAB	0.0088166	74.18	-0.00426803	29.21	123
SUPNAS	-0.0024757	0.16	-0.00103430	0.05	1
PNAS	0.04353835	11.9	0.02090095	4.6	4
PMENT	-0.00320609	1.53	0.02343897	9.0	7
BRIL	0.00133865	3.69	0.00224311	5.12	41.5
FTL	0.00150731	1.69	0.03762565	34.92	16.5
GETE	0.00227635	6.85	0.00672431	17.10	45.5

Figure 32. Direction and magnitude of influence of characters used in multivariate analysis of variance. Abbreviations are as in Table 18, p. 171. Abscissa represents canonical variate II, ordinate represents canonical variate I.


SAB
PNAS
BRIL
GETE
FTL
PMENT
SUPNAS
CV 2
CV 1
+
70
60
50
40
30
20
10
10
-
-
30
20
10
10
20
30
+

character. Characters with greatest percent influence (e.g. largest magnitude in Fig. 32; SAB) serve best to distinguish among samples. Two characters (FTL and GETE) exert considerable influence in defining samples. All other characters are less significant for that purpose. The characteristic roots and percentage of the variation accounted for by each canonical variate are given in Table 19.

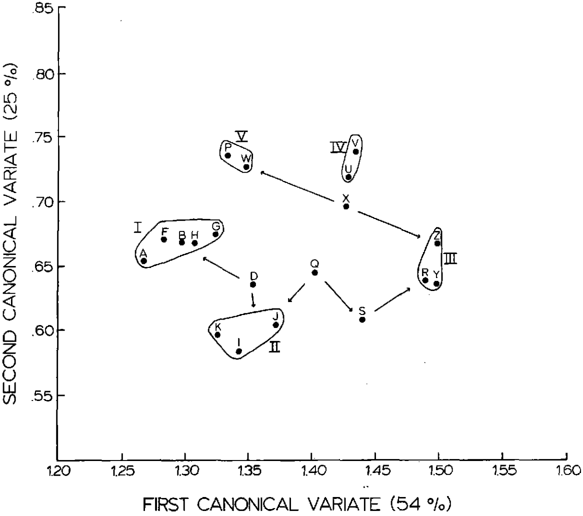
A graphic display of canonical variates I and II (Fig. 33) illustrates affinities among samples based on seven characters considered simultaneously. The two canonical variates account for approximately 80% of the total variation within the species. The first canonical variate (abcissa) separates populations most different throughout that axis. The most significant result is the separation of New Mexico and Trans-Pecos Texas populations (ABFGH) from Rio Grande Valley populations (YZ). The second canonical variate (ordinate) partitions populations most distinct on that axis; the Mesa del Norte populations (UV and PW) and the Pecos River populations (IJK) are recognized as quite distinct.

MANOVA suggests that populations tend to fall into five well-defined groups (Fig. 33). Populations that exhibit close affinity are circled. Intermediate populations are noted and arrows showing possible affinities with circled groups are included. Group I includes specimens from Eddy and Otero counties, New Mexico and Brewster, Jeff Davis, and Presidio counties, Texas.

Table 19. Characteristic roots and percentages of variation accounted for by canonical variates I-VII.

Canonical Variates	Characteristic Roots	Percent	Cumulative Percent
I	1.60083973	54.36	54.36
II	0.74877641	25.43	79.79
III	0.20371419	6.92	86.71
IV	0.17673505	6.00	92.71
V	0.10561305	3.59	96.30
VI	0.07251100	2.46	98.76
VII	0.03660867	1.24	100.00

Figure 33. Plot of means of pooled samples (cf. Fig. 25, p. 131) for canonical variates I and II. Black lines surround pooled samples considered as major groups. Black arrows show affinities of intermediate samples with major groups.


SECOND CANONICAL VARIATE (25 %)
.85
.80
.75
.70
.65
.60
.55
1.20
1.25
1.30
1.35
1.40
1.45
1.50
1.55
1.60
FIRST CANONICAL VARIATE (54 %)
I
A
F
B
H
G
II
K
I
J
III
Z
R
Y
IV
V
U
V
P
W
X
D
Q
S

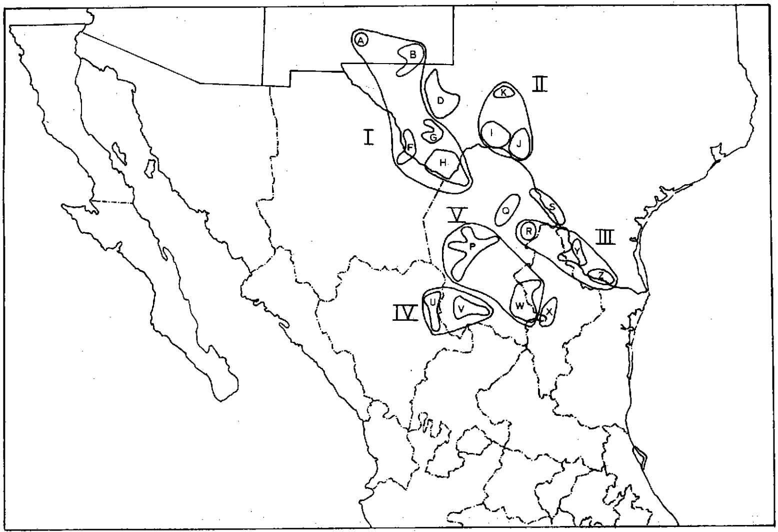
Group II includes specimens from Reagan, Terrell, and Val Verde counties, Texas. Intermediate between groups I and II (graphically and geographically) is area D (Pecos County, Texas). The Rio Grande Valley populations aggregate in group III. Area S (Webb County, Texas) is graphically and geographically intermediate between groups II and III. Of interest is area Q, graphically quite near to group II. Geographically, area Q is proximate to area R (group III), but as shown in univariate analysis, Q is more closely related to areas I and J to the north. That the populations in group III fall together supports evidence presented in univariate analysis. Group IV includes areas U and V, geographically very proximate. Area X falls out approximately half way between groups V and III. However, geographically area X is quite close to area W. The graphically intermediate position suggests distinction from area W and supports conclusions derived in univariate analysis. That X is graphically nearest to group IV is probably a function of small sample size. Graphically, group V separates considerably from groups IV and I. Populations in groups IV and I are geographically close to group V. The chasm illustrated between groups IV and V suggests reduced gene exchange between the two areas. This supports evidence presented in univariate analysis.

Small sample size in some populations and lack of specimens from strategic areas between major groups render the conclusions as generalizations. However, certain trends with respect to variation can be accepted. From the data, it appears that there are no continua between major groups illustrated in Fig. 33, p. 177. Further specimens may fill in the gaps. However, groups that fall out distinctively (i.e., group II from I, group V from IV) suggest a demic status. Intermediate populations (area Q near group II, area S intermediate between groups II and III, area X intermediate between groups III and V) suggest genetic connections between the more local concentrations (e.g. groups in Fig. 33, p. 177).

The local concentrations can be more fully visualized geographically (Fig. 34). Generally, groups I through V cluster in a fashion similar to that in univariate analysis. The Trans-Pecos Region, considered one group in univariate analysis, divides into two in MANOVA. The Rio Grande Valley group in MANOVA coincides with a similar grouping in univariate analysis. Central and southeastern Coahuila populations separate from Trans-Pecos populations in MANOVA; in univariate analysis the Coahuila populations both group and separate from the Trans-Pecos populations. As in univariate analysis, the southwestern Coahuila and Durango populations separate nicely from central Coahuila populations.

The support that MANOVA lends to univariate analysis is conclusive with respect to general evolutionary trends within the species. Further specimens, especially from areas intermediate between groups in Mexico, should bring the description of geographic

Figure 34. Major groups (I-V) of *Coleonyx brevis* as designated by canonical variates I and II in a multivariate analysis of the data. Pooled samples enclosed in heavy black lines form major groups. Pooled samples that are intermediate graphically (cf. Fig. 33, p. 177) are not enclosed in heavy black lines.


A
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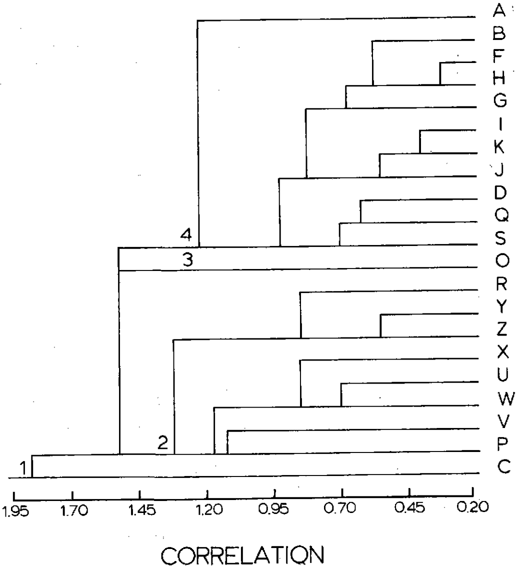
variation into sharper focus.

Cluster analysis. A dendrogram illustrating the phenetic relationship of 21 samples with complete data was computed from a correlation matrix. Values from the seven squamative characters used in canonical variate analysis were considered in forming the matrix. The correlation phenogram (Fig. 35) illustrates that samples separate into four major groups. Group 1 (area C), geographically proximate to group 4, falls out first and the separation may be attributed to small sample size. Likewise, group 3 (area O), though intermediate between groups 2 and 4 phenotypically and geographically, is represented by a small sample. Groups 2 and 4 accurately represent major phenotypic relationships among samples of *C. brevis*. Group 2 includes all samples along the southern border of the Mesa del Norte, Cuatro Cienegas, Coahuila, the Rio Grande Valley, and one population from the Gulf Coastal Plain (area R). Group 4 includes all samples from New Mexico, Trans-Pecos Texas, the Pecos River area, and Webb County, Texas.

As with major groups, subgroups illustrated in Figure 35 show geographic conformity. In group 4 geographically proximate populations (Brewster, Presidio, and Jeff Davis counties) fall out together as do Terrell, Val Verde, and Reagan counties, Texas populations. The Villa Union, Coahuila (area Q) population clusters with the Webb County, Texas (area S) population. In group 2, the Don Martin Dam population (area R) clusters with the Rio Grande

Figure 35. Correlation phenogram of 21 samples of *Coleonyx brevis* based on seven squamative characters.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3
2
1
1.95
1.70
1.45
1.20
0.95
0.70
0.45
0.20
CORRELATION

Valley populations (areas Y and Z). All populations from the southern portion of the Mesa del Norte (areas PUVWX) group together. In general, cluster analysis lends support to trends noted in multivariate and univariate analysis.

Taxonomic Considerations

Conclusions reached by a systematist are derived from documentation of geographic variation of a species and correlation of the variation with climatic, environmental, or physical factors. Interpretation of the data, the personal expression of the systematist, should be conclusive and sound. In a time when even the species concept is being questioned (and with basis), many disagree on the use of the trinomial in classification. However, ideologically and pragmatically, it is quite useful (see Durrant, 1955).

Mayr's (1970) definition of a subspecies approaches the concept accurately. "A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species." The term "differing taxonomically" leaves much to the interpretation of the worker.

Univariate analysis of the data has revealed clinal variation in six characters and suggested certain groupings for populations of *C. brevis*. Relations among populations in areas of physiographic diversity were demonstrated. The multivariate analysis and cluster analysis revealed relationships among the samples and populations in much the same fashion as the univariate analysis.

In some respects the analysis is weakened by small sample size and lack of material from strategic areas. However, some general evolutionary trends within the species have been suggested.

It is interesting that areas Q and R are so different. This probably represents limited gene exchange between the two areas as a result of unsuitable habitat (i.e., grasslands). It appears that evolutionary activity is occurring resulting in at least a demic status of groups I and II and groups IV and V (Fig. 33, p. 177). Possibly, physiographic barriers are restricting gene exchange between these groups, resulting in their divergence. If additional specimens reveal that group I is quite distinct from II and group IV is quite distinct from V, then perhaps a trinomial designation will be warranted. However, this must await additional specimens and further analysis. It is concluded that groups I through V have not reached the status of subspecies. Therefore, at this time, they are referred to as contiguous geographic demes.

Zoogeography

The discussion on the evolution and zoogeography of Coleonyx is mainly a synthesis of ideas postulated by Kluge (1967) and numerous authors on paleobiogeography.

The gekkonid subfamily Eublepharinae is represented by a discontinuous distribution of five relect genera. Two genera (*Aeluroscalabotes* and *Holodactylus*) occur in the Oriental Region, two (*Eublepharis* and *Hemitheconyx*) in the Ethiopian Region, and one (*Coleonyx*) in southwestern North America and Central America. All genera (except *Aeluroscalabotes*) inhabit arid areas. In his study on the evolution of the Gekkonidae, Kluge (1967) presented data illustrating the primitiveness of the Eublepharinae and possible phyletic relationships of the subfamily to the three additional (more advanced) subfamilies.

The ancestors of the present members of the Eublepharinae probably evolved during the Upper Jurassic or Lower Cretaceous. Early evolution of the subfamily probably took place in southeast Asia in association with tropical conditions of the Tertiary (Kluge, 1967). The genus *Aeluroscalabotes* (forest species, southeast Asia) represents the type of eublepharine from which all other genera arose. Dispersal of the *Coleonyx*-type lizard to the Western Hemisphere occurred during the Tertiary. Therefore, the original radiation of genera from the *Aeluroscalabotes*-type lizard occurred probably in the late Cretaceous (Kluge, 1967). *Coleonyx* almost certainly evolved directly from an *Eublepharis*-like ancestor (Kluge, 1962). The ancestors of *Coleonyx* arrived in the Western Hemisphere via the Bering Land Bridge through subtropical conditions of the Paleocene (Axelrod, 1958; Kluge, 1967).

Modern Coleonyx are represented by two species groups: (1) the nontubercled group of C. variegatus and C. brevis and (2) the tubercled group of C. mitratus, C. elegans, and C. reticulatus. All of the nontubercled forms occur in the arid areas of southwestern United States and northern Mexico. Two of the tubercled species occur only in forested areas of southern Mexico and Central America, and one occurs in arid areas of west Texas and northern Mexico. Kluge (1962) demonstrated that the tubercled species are more closely related to the modern Eublepharis than are the nontubercled species.

Between the Pliocene and the Pleistocene considerable desert-steppe areas developed in northern Mexico and southwestern United States (Braun, 1955); the region was characterized by low rainfall, high summer temperatures, and long periods of sunshine from Early to Late Tertiary (Axelrod, 1958). The Sonoran, Mojave, and Chihuahuan Deserts developed during the expansion of arid conditions following the Eocene. Eastern Hemisphere deserts (Africa, Pakistan, India) developed concurrently. It is probable that the Western Hemisphere ancestor of Coleonyx was present in pre-desert habitat in southern Mexico and Central America. As deserts were formed the variegatus-brevis stock adapted to and invaded xeric habitats (Kluge, 1967). This is supported by Savage's (1960) idea that the chapparal and subtropical scrub habitat of the more primitive nontubercled subspecies of *Coleonyx* (*C. variegatus abbotti* and *C. v. peninsularis*) may be indicative of the pre-desert (subtropical) habitat of the ancestral stock. Kluge (1967) states that the southern tubercled group occurs in what is believed to be a derivative of the ancestral tropical flora of the Western Hemisphere in which the genus evolved. He concludes that the forest forms of *Coleonyx* (southern tubercled) may be more closely related to *Eublepharis* (the ancestral form) than to the desert, nontubercled forms of *Coleonyx*.

Parallel evolution has resulted in apparent ecological equivalents between four of the five genera of eublepharine geckos. The four inhabit arid areas in the Eastern and Western Hemisphere and probably fill similar ecological niches.

That *C. reticulatus* is more closely related to the forest, tubercled forms is supported by the data on thermal ecology. The species prefers temperatures considerably lower than the sympatric species, *C. brevis*, and than most other desert species. Lower temperatures are associated with more mesic, tropical habitats (Ballinger et al., 1970). Bogert (1949) emphasized the ability of lizards to find suitable habitats in temperate areas while maintaining body temperatures preferred by their ancestral groups. Inger (1959) stated that preferred (eccritic) body temperatures are evolved early in the history of most species. It is suggested that the lower preferred body temperature of *C. reticulatus* reflects its close relation with the tubercled forest species. Furthermore, the prehensile tail probably reflects adaptation to a more arboreal life (Stebbins, 1966) which would be expectated in originally forest dwelling species. Seemingly, C. reticulatus is a relict species that originally occurred in what was once a subtropical forest habitat, and has adapted to a desert habitat as the environment has changed. However, it should be emphasized that the foregoing statement is, for the most part, speculation and any conclusions must await further investigations.

Auffenberg and Milstead (1965) have suggested that with each glacial age sea level has lowered while with each interglacial period it has risen. Such fluctuations have considerable influence on the geographic range of species living in coastal areas. The Gulf Coastal Plain area has been below sea level at least as late as the Eocene. By altering edaphic and vegetative characteristics, such changes in sea level possibly could have been instrumental in effecting geographic variation among populations of C. brevis that eventually occurred in the area. Furthermore, the Pliocene uplift of the Sierra Madre Oriental since may have caused the separation of populations in the Gulf Coastal Plain and the Mexican Plateau. Fingers of suitable habitat radiate through passes throughout the Sierra Madre Oriental, potentially connecting populations of the Mexican Plateau and the Gulf Coastal Plain. However, if C. brevis on the Gulf Coastal Plain has developed into a different ecotype than on the Plateau, separation by habitat selection may be causing some reproductive isolation between the two types, thus allowing the divergence noted.

SYSTEMATIC ACCOUNT

Synonomy

The format lists all new descriptions and first combinations.

Coleonyx brevis Stejneger

Stenodactylus variegatus Baird, 1859: 254.

Coleonyx variegatus: Cope, 1880: 13.

Eublepharis variegatus: Boulenger, 1885: 233.

Coleonyx brevis Stejneger, 1893: 163.

Coleonyx variegatus brevis: Schmidt, 1953: 114.

Holotype and Type Locality

Holotype: U.S. National Museum 13627, collected 30 November 1883, by G.W. Marnock.

Type Locality: "Helotes, Bexar County, Texas" (= Marnock's Ranch on Helotes Creek, 29° 35' N - 98° 41' 15" W, approximately 22 miles northwest of San Antonio, Texas, according to Strecker, 1933).

Distribution

Coleonyx brevis occur in parts of the Chihuahuan Desert, the Balconian Biotic Province (Blair, 1950), and the Tamaulipan Biotic

Province (Goldman and Moore, 1946; Blair, 1950). The species ranges from southeastern New Mexico, into Texas, and into Chihuahua, Durango, Coahuila, Nuevo Leon, and Tamaulipas, Mexico. *Coleonyx brevis* prefers xeric to semi-xeric habitat with rocky or gravely soils.

Diagnosis

Coleonyx brevis is a small lizard, with a maximum snout-vent length of 63 mm. The species has: three to six preanal pores, one to five scales between preanal pores, and no enlarged dorsal tubercles. The base of the cloacal spur is not constricted, and its distal end is flat.

Description

Klauber (1945) described the species rather aptly. The following description is taken, in part, from him.

The head is wedge-shaped and somewhat blunt. The nostrils are circular. The ear openings are large and are elliptical in shape. The eyelids are functional and are interiorly pigmented with black.

The head is covered, dorsally and ventrally, with granules, except for the borders of the mouth, nostrils, and eyes. The mental is the largest of the head scales. It is wider than long, and the posterior border is semi-circular.

The rostral, the second largest head scale, is pentagonal, with concave sides contacting the supranasals. The supranasals are lunar in shape and are wider dorsally. The supranasals may be separated medially by a granule. The postnasals are smaller, and are widely separated from postnasals on the opposite side of the head by granules. Postnasals border the nostril on the dorsal, posterior, and ventral sides.

Supralabials and infralabials decrease in size posteriorly; posterior supralabials and infralabials are granular in size.

The eyelids are bordered with extrabrillar fringe scales. Such scales vary from short, blunt scales, to elongate scales with curved, pointed tips.

Gular scales are granular in size and extend from the posterior border of the mental throughout the gular region.

The dorsal surface of the body is covered with granules. The ventral surface of the body is covered with scales that are somewhat imbricate and are slightly larger than the dorsal granules.

The tail is covered with rows of imbricate scales. The limbs are covered with both imbricate and granular scales. The digits are sheathed with overlapping scales. The lower surfaces are covered with imbricate scales which form the lamellae. The claws are housed between two large, lateral shell-shaped scales, capped above by a long, thin, pointed scale.

Synonomy

Coleonyx reticulatus Davis and Dixon

Coleonyx reticulatus Davis and Dixon, 1958: 151.

Holotype and Type Locality

Holotype: Texas Cooperative Wildlife Collection 12855, collected 20 June 1956, by Charles K. Winkler.
Type Locality: "Black Gap, 50 miles south-southeast of Marathon, 2,500 ft., Brewster County, Texas."

Distribution

Coleonyx reticulatus occurs in parts of the Chihuahuan Desert in Texas and Durango, Mexico. The species is known only from several localities in Brewster and Presidio counties, Texas and 7 mi. southwest of Leon Guzman, Durango, Mexico.

Diagnosis

Coleonyx reticulatus is a large gecko with a maximum snout-vent length of 94 mm. The species has: 13 to 16 longitudinal rows of dorsal tubercles, 18 to 20 preanal pores, no scales between preanal pores, and 23 to 31 fourth toe lamallae.

Description

The following description is taken, in part, from the original description by Davis and Dixon (1958).

The head is wedge shaped and rather blunt. The nostrils are circular and the ear openings are large and ellipsoid. The eyelids are functional.

The head is covered, dorsally and ventrally, with granular scales, except for the borders of the mouth, nostrils, and eyes. The mental is the largest of the head scales.

The nostril is pentagonal and the sides border the nostril posteriorly and the supranasals dorso-posteriorly. The supranasals are lunar in shape and are wider dorsally. The supranasals may be separated medially by one or two granules. The postnasals are smaller and border the nostril dorso-posteriorly, posteriorly, and ventrally.

Supralabials and infralabials decrease in size posteriorly. The eyelids are bordered with extrabrillar fringe scales. Gular scales are granular in size and extend from the posterior border of the mental throughout the gular region.

The dorsal surface is covered with granules similar in size to those on the head. Interspersed on the dorsum are 13 to 16 rows of tubercles. The ventral scales are somewhat imbricate and are larger than the dorsal scales.

The tail is covered with rows of imbricate scales. The limbs are covered with granules similar in size to those on the dorsum. The digits are sheathed with overlapping scales. The lower surfaces are covered with imbricate scales which form the lamellae. The claws are housed between two large, lateral shell-shaped scales.

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APPENDIX

SPECIMENS EXAMINED

Coleonyx brevis

UNITED STATES. *New Mexico*: Eddy Co. (LACM 3242, 3243, 93416, UNM 7217, 7218, 7219, 17819, 17820, 25807, 25846, 25922, 25947, 25948, 25976, 26004, 26033, 26088, 26109); Otero Co. (UNM 6739, 6740, 6741, 6742). *Texas*: Bexar Co. (SM 0853, 5208, 5650); Brewster Co. (BCB 8546, BED 282, 289, 290, 283, 284, 291, 285, 286, 287, 294, 295, 298, 299, 300, 301, 302, 305, 306, 307, 308, 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 326, 327, 328, 329, 330, 331, 332, 333, 334, 335, 337, 340, 341, 344, 345, 346, 347, 350, 353, 354, 355, 360, 361, 362, 363, 364, 365, 366, 367, 368, 369, 370, FWMSH 5527, UNM 6383, 6384, 6385, 6386, 6387, 6388, 6553, 6554, 9933, 16683, 16684, 17175, 17176, 17177, 17178, 18336, 18337, 18338, 18339, 18340, 18341, 18342, 18343, 18344, 18345, 18346, 18347, 18348, 19183, 19184, 19954, 19955, 19956, 19957, 19958, 19959, 19960, 20850, 20851, 20852, 20853, TCWC 1111, 3197, 5446, 5447, 5448, 5449, 12854, 15951, 15952, 15953, 15954, 15955, 15956, 15957, 15958, 15959, 15960, 15961, 17962, 26101, 26102, 36969, 39911, 39912, TNHC 12515, 12566, 12567, 12568, 12584, 12585, 12586, 12607, 12620, 12628, 12658, 12684, 12685, 12728, 12768, 12769, 12770, 12771, 12787, 12788, 12805, 12816, 12817, 12843, 12867, 12876, 12880, 12881, 12882, 12904, 12905, 12942, 12951, 12952, 12976, 12746, 12890, 20821, 21613, 21614); Crockett Co. (SM 11308); Culberson Co. (BCB 8842); Ector Co. (FWMSH 2440); Edwards Co. (BCB 8841); Hidalgo Co. (BCB 1644, 1647, BED 372, 373, 374, SM 8494, 8495, TCWC 17961); Hudspeth Co. (TCWC 36596); Jeff Davis Co. (FWMSH 2441); Loving Co. (BCB 14700, SM 7566, 7558, 7559, TCWC 23369, 23370, 23371, 23373, 23374); Pecos Co. (UNM 6000, TCWC 26103, 39910); Presidio Co. (FWMSH 7470, TCWC 27871, 27872, 27873, 29360, 29361, 26105, 26106, 26107, 27586); Reagan Co. (SM 8838, 8839, TCWC 31290, 31291, 31292, 31293, 31294, 31295, 31296, 31297, 31298, 31299, 31300, 31301, 31302, 31303, 31304, 31305, 31306, 31307, 31308, 31309, 31310, 31311, 31312); Reeves Co. (UNM 26405); Starr Co. (BCB 4840, 3841, 4838, SM 8498, FWMSH 2620, 2621, TNHC 96, 97, 1466, 1467, 1468, 1469, 8888, 8889, 8890, 8891, 8892, 8893, 8898, 8899, 8900, 13500, 23138, 23139); Terrell Co. (SM 8496, TCWC 39900, 39901, 39902, 39903, 39909); Uvalde Co. (BCB 11380, 11378); Val Verde Co. (BCB 8838, 8106, 8104, 8107, 8103, BED 324, 325, 377, 378, 379, 380, 381, 382, 383, FWMSH 7394, TCWC 432, 5445, 5450, 5451, 5452, 13766, 20380, 21591, 26104, 38866, 38867, 38868, 38869, 38870, 38871, 38872, 39879, 39880, 39881, 39882, 39883, 39884, 39885, 39886, 39887, 39888, 39889, 39890, 39891, 39897, 39898, 39899, 39904, 39905, 39906, 39907, 39908, TNHC 220, 222, 223, 225, 226, 227, 228, 229, 230, 231, 232, 236, 237, 238, 239, 11683, 11684, 11692); Webb Co. (BCB 7940, 7942, 7939, 7944, 7945, TCWC 14630, 14631, 14632, 14633, 14634, 14635, 34992, 34993, 34994, TNHC

5879, 5880, 5881, 5882, 5883, 5884, 5885, 5886, 5887, 5888, 5889, 5890, 5891, 5892, 29261); Zapata Co. (BCB 3472, 3464, FWMSH 5576, 5577, 5578, 5579, SM 5724, TCWC 17963, TNHC 1471, 1472, 1473, 1474, 1475, 1476, 13499, 8896, 8897, 20378, 20379, 23136, 23137).

MEXICO. Chihuahua: (UIMNH 48292, KU 33874, TCWC 43798); Durango: (UIMNH 43372, 43365, 43364, 43368, 43366, 43367, 43370, 43369, KU 39905, UMMZ 131663, TCWC 42995, 42996, 42997, 42998, 42999, 43000, RGW 3286, 5395, 5682, 5683); Coahuila: (FWMSH 6208, 6209, 6210, UIMNH 19526, 43363, 43371, 48293, 43362, 6661, KU 38309, 39903, 39904, 56167, 128814, 128815, 128816, 128817, 128818, 128819, 128820, 128821, 128822, 128823, UMMZ 112926, 118962, TCWC 36618, 36621, 38916, 38917, 38918, 38919, 38920, 42993, 42994, 43001, 43002, 43003, 43799, 43800, 43801, 43802, 43803, 43804, 43805, 43806, 43807, 43808, 43809, 43810); Nuevo Leou: (UIMNH 6665, 6663, 19531, KU 67461, 67462, 128824, UMMZ 119035, TCWC 38921, 44342).

Coleonyx reticulatus

UNITED STATES. Texas: Brewster Co. (BBNP 4262, BED 292, 348, DMNH 794, 795, 969, 1157, 1158, LACM 93432, 101266, TCWC 12855, 39330, 39331, 39332; Presido Co. (DMNH 970, TCWC 39333, 39334).

MEXICO. RGW 5396.

VITA

Benjamin Edward Dial was born on October 23, 1944 in Atlanta, Georgia to E. Lamar Dial and Helen Jones Dial. He graduated from R.L. Turner (Carrollton) High School, Dallas County, Texas in June, 1962. He attended Texas A&M University, College Station, Texas from September, 1962 to June, 1963, the University of Texas at Arlington, Arlington, Texas from September, 1963 to December, 1964, and Texas A&M University from January, 1965 to June, 1968. From June, 1969 to August, 1971 he was employed by Coghill-Simmons Music Co., Dallas, Texas and from September, 1971 to December, 1971 by the J.C. Penney Co., Dallas, Texas.

In January, 1972 he returned to Texas A&M University and received his Bachelor of Science degree in Wildlife and Fisheries Sciences in December, 1972. He began his graduate studies in the Department of Wildlife and Fisheries Sciences at Texas A&M University in January, 1973.

Mr. Dial has served at Texas A&M University as a curatorial assistant for the Texas Cooperative Wildlife Collection (summer, 1973), as a Teaching Assistant (spring-1972, 1973, 1974), and as a Graduate Research Assistant (June, 1973-October, 1974).

His permanent mailing address is 2854 Duval Drive, Dallas, Texas 75211.

The typist for this thesis was Mrs. James Albert.

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