A Annotated Bibliography
of the
Genus Cyphophorus in New Mexico

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INTRODUCTION

The Teiid lizard genus Cnemidophorus attains its highest diversity in North America within the borders of the state of New Mexico. Lizards of this genus are dominant components of the terrestrial fauna, yet their biology is only now being understood. Indeed, with one notable exception, little was known about the North American species twenty years ago except that they were highly confusing taxonomically. Then, this genus was discovered to be unique among vertebrates with its high proportion of unisexual taxa. Fully one-half of the forms in New Mexico are obligate parthenospecies; each of these is derived from hybridization events between two or more sexual species of the genus. They are clonally diverse in some cases, perhaps all; that is, they manifest genetic and morphological variability somewhat approaching that of sexual species although localized populations are usually quite homogeneous. The ecological and evolutionary interactions of these parthenospecies with each other, and with their sexual congeners, is only now being detailed.

One cannot study this genus without coming to grips with the labyrinthine snarl of its taxonomy. Systematic solutions have spanned the gamut from minute detailing of non-significant variation to simply ignoring differences. The genus is a diverse one, and much of the confusion resulted from an unawareness of hybrid parthenogenetic clones within it. Morphological characters can be more or less variable in clones than in sexual populations, depending upon the character and the scope of the examination. The parthenospecies considered here do present a taxonomic problem. The biological species concept, which requires free intraspecific exchange of genetic material, obviously does not apply to them. They just as obviously exist. How does one deal with them on a taxonomic basis? Again, solutions ranged from giving each separate clone specific rank to taxonomically ignoring them. I agree with Maslin, Wiley and others that each successful parthenogenetic clone does have an evolutionary life span and with the modification of Simpson's evolutionary species concept to include them. I propose a further step. One has to know what organisms one is dealing with in order to do biology well. This is part of the fundamental utility of the biological species concept, yet it has not been applied to parthenogenetic Cnemidophorus without ambiguity, confusion, and controversy. The capability exists, detailed in this bibliography, to identify the parental sexual species of each parthenospecies of Cnemidophorus. I propose that a given species name be applied and restricted to a particular combinatorial sequence, past, present or future, of successful hybridization events. Thus, the name Cnemidophorus neomexicanus will be uniquely applied to clones originating from C. inornatus X C. tigris events. This will obviate the necessity of applying multiple names to a clonal species complex (Zweifel's pattern class system will serve admirably in this regard) and of naming (or ignoring) aberrant individuals representing chance hybrid events that do not represent successful populations. Most important, I believe this scheme
provides an evolutionary foundation to the nomenclature of parthenogenetic Cnemidophorus, which can only aid in the understanding of their biology. I believe that C. dixoni is not a valid parthenospecies based on these criteria. It was originally erected on the basis of color pattern and ecological differences, which are not sufficient criteria for recognizing species. It is obviously a C. tesselatus clone, with its own particular ecological requirements and evolutionary history, and differing no more from other clones of that species than they do from each other. I believe that C. dixoni should be, and will do so formally in a future paper, relegated to the synonymy of C. tesselatus.

It is apparent that each species, sexual or parthenogenetic, has its own particular set of ecological requirements and, given historical factors, will occur wherever these requirements are satisfied. These requirements are not yet fully understood and appear to lead to a bewildering array of discontinuous, overlapping species assemblages. It is also apparent that at least some parthenospecies have had multiple origins but that not every hybridization event has generated a successful parthenogenetic population because aberrant individuals representing probable hybrids are collected regularly. The cytogenetic criteria necessary for parthenogenetic reproduction are not understood. The ecological conditions required for parthenogenetic populations to succeed are beginning to be investigated; this bibliography provides a body of uncorrelated data and opinion on that subject. The species of Cnemidophorus in New Mexico provide a rich, fertile ground for the study of many biological phenomena. I believe that the species themselves and their interactions can be utilized as excellent indices of present habitat type, condition and environmental quality, and that of the historically recent past. Much interesting and potentially significant field work remains undone.

The following index is a numerical listing of the annotations by species. Parthenospecies are designated (P). A citation number is placed after a particular subspecies name when it is known definitively that that subspecies is referred to; otherwise the number is placed after the general species name. Correct species names are placed in parentheses in the text following names that are no longer in use or that are incorrectly applied. The bibliography is not exhaustive; I have omitted such as the popular Field Guides which are readily available to everyone, and works of a purely taxonomic nature which are either useless or not pertinent to the scope of this work. The bibliography is nevertheless complete; it represents the sum total of the knowledge on the species of Cnemidophorus that occur in New Mexico.

ACKNOWLEDGEMENTS

I wish to thank Holly Reynolds and the Interlibrary Loan Staff at New Mexico State University for graciously tracking down obscure and/or hard-to-get papers. Dr. C. J. McCoy of the Carnegie Museum of Natural
History also helped in this regard, as well as providing encouragement. I particularly wish to thank Wirt and Valerie Atmar, and AICS, Box 4691, University Park, Las Cruces, New Mexico, for the use of a System 2000 Terminal and Word Processor with which this bibliography was composed. Most importantly, I wish to thank my wife Weslyn and son Alec for their kindness and tolerance. I thank her and Wirt Atmar for their efforts on the cover illustration. This bibliography was done under contract 519-70-06 for the Endangered Species Program, New Mexico Department of Game and Fish, and I thank Bill Baltosser in particular for his help and consideration.
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BIBLIOGRAPHY


* Cnemidophorus tigris tigris * hosted Odontacarus arizonensis and Eutrombicula belkini. Areas of greatest infestation were in the directions of fallout from nuclear detonations.


Daily energy metabolism and water flux were measured with doubly labeled H$_2$O in free-living Cnemidophorus tigris in the Colorado Desert of California. 91% of the 5-hour active day is spent in movement. The costs of free existence were calculated from the difference between field metabolism rates and maintenance costs estimated in the laboratory. *C. tigris* was found to be energy efficient.


Individual Cnemidophorus tigris, when active near the eccritic body temperature, (1) consume over 2 cc of oxygen per gram-hour, more than a resting mammal of the same size, (2) attain body temperatures 1-2 degrees Centigrade above ambient if they weigh 80-100 grams. These properties are similar to but much greater than those of varanid lizards. Thermogenesis (muscular activity) could play a role in the thermal ecology and habitat selection of macroteiid lizards.


This study involved field and laboratory manipulations of subspecies of Cnemidophorus tigris of varying sizes, including C. tigris gracilis. Whiptails have the highest known sustained rates of oxidative metabolism among reptiles. Body size plays a relatively direct role in determining the thermospatial niche of these lizards. Larger lizards bask less and spend more of their activity period in the shade than do smaller lizards with the same thermal preferenda and tolerance limits. Variation of body size in Cnemidophorus may reflect adaptation
to differences in desert vegetation structure; relatively larger lizards being more successful in relatively shaded habitats. Small body size may be of selective advantage during decreases in vegetation density or during increases in the extremes or instabilities of climate.


The area is described and ecological differences between Cnemidophorus inornatus heptagrammus and C. tigris marmoratus are discussed.


The nomenclatural confusion surrounding the lizard now known as Cnemidophorus inornatus is reviewed. The subspecies C. i. inornatus and C. i. heptagrammus (occurs in our area) are formally named, diagnosed, and described. Their respective habitats and distributions are discussed, and range maps are provided.


The taxonomic history of the species is briefly reviewed, and a detailed range map is provided. Ecological attributes and interactions of this species with others in the genus are discussed in detail. Two presumed hybrids between C. neomexicanus and C. inornatus are described. The geographic fragmentation of southern populations of C. neomexicanus is explained in light of the geologic history of the area and a Wisconsin or pre-Wisconsin time of origin is suggested for the species.


The geomorphic history of the region in Chihuahua and New Mexico is considered in detail. Western range margins of Cnemidophorus tessellatus and C. tigris marmoratus. southern range margins of C. inornatus
and *C. neomexicanus* (map presented), and eastern range margins of *C. tigris gracilis* appear to have been influenced by various lacustrine barriers. Records for *C. neomexicanus* in the Jornada del Muerto, but not in the Elephant Butte Basin, support contentions that the ancestral Rio Grande once flowed through the former; Quaternary basalt flows in the middle Jornada are believed to have diverted it westward through the Elephant Butte Gap.


Evidence suggesting possible gene exchange between *C. exsanguis* and *C. septemvittatus scalaris* is discussed.


Species examined were *exsanguis, gularis, inornatus, tessellatus* and *tigris*. It is suggested that hemoprotozoan diseases are not important population regulating factors here as they are in natural populations elsewhere.


Values of caloric and water content for eggs of *Cnemidophorus gularis* and *C. sexlineatus* are given. The determination of reproductive effort is briefly discussed.


A photograph and description of *Cnemidophorus tigris marmoratus* from Crane County, Texas, is given.

Running speed was reduced by an average of 36% by removing tails in lizards collected in Nebraska. Tail autonomy occurs less frequently and less easily in lizards that utilize speed for escape, such as this species, than in species that utilize tail-breakage for escape.


The reproductive cycles and size and age at maturity are discussed for a population near San Angelo, Texas. As many as 50% of the females do not mature until their second reproductive season. Those that mature during their first season do so late and lay one clutch of 3-4 eggs. Older females lay 2 clutches per year averaging 5 eggs each.


*C. tigris* is active on a daily basis in July between 0900 and 1700 hours with peak activity occurring at 1300 hours. Activity graphs presented show the species to be more active on cloudy than sunny days. Cloacal temperatures of active lizards average 37.13°C, with average air and soil temperatures of 27.46°C and 34.76°C, respectively. It is suggested that density estimates based on line transect data be made over many days and times of varying environmental conditions to be valid.


*Cnemidophorus tigris* and *C. inornatus* are optimally specialized to eat termites, but are essentially opportunistic feeders with highly diversified and largely overlapping diets. *C. inornatus* avoids competition by living in a specialized microhabitat (*Hilaria mutica* communities).


This study investigates niche relationships among the 11 main diurnal insectivorous species of the lizard community in the Mapimi desert near Ceballos, Durango, Mexico. *C. inornatus* and *C. tigris* were
among the species studied. Time of activity, habitat, and food were
the niche gradients measured. There appears to be a high overlap be-
tween C. tigris and the third teiid species present, C. scalaris. Close
observation of their ecologies at a finer level reveals many small
differences between them, and these are examined. They may be
assumed to be potentially competitive. Frequent interspecific aggres-
sive encounters occur in the field in which C. tigris always chases C.
scalaris away. It is suggested that in a highly heterogeneous, unpre-
dictable ecosystem like the Mapimi the small ecological differences
mentioned greatly facilitates the coexistence of these two species.
It is further suggested that the very diversified ecological opportu-
ism of C. scalaris allows it to colonize periodically the ecosystem
where C. tigris is dominant in only a small number of biotopes.

18. Barden, A. 1942. Activity of the lizard, Cnemidophorus sexline-
atus. ECOLOGY 23(3): 336-344.

Laboratory experiments were done on lizards from Kansas and Indi-
ana to elucidate potential parameters controlling activity. Activity
rhythms are partially endogenous and partially controlled by environ-
mental factors such as light and temperature, with increasing day length
implicated as triggering spring emergence from hibernation.

genus Cnemidophorus. PH.D. DISS., UNIV. OF COLORADO. 175 p.

The abstract is not informative, but the work is probably perti-
nent to this report. The author cannot afford to purchase it, and the
University of Colorado will not lend the work.


12 lizards, C. t. mundus and C. t. tigris, were trained to feed
against a background of colored discs. The lizards were divided into
two equal groups and individuals were presented with a pair of discs
from which to feed. One group fed undisturbed from red discs and was
given an electric shock when attempting to feed from green ones; the
other group underwent the reverse procedure. The initial disc pair was
quite divergent in color; the pairs became closer and closer in color
to each other on successive trials. The lizards in each group learned
from which color disc they could feed successfully. Red colors tend to
be less acceptable and green colors more difficult to learn to reject
than the reverse situation. Cnemidophorus tigris can make fine distinc-
tions in color differences and is also capable of a generalized color
reaction. It is suggested that warning colors of unpalatable prey can
be associated with unpalatability or noxiousness with experience by the lizard and that the association formed could also be transferred to other not necessarily unpalatable insect species of similar colors.


An analysis of the stomach contents of a seasonally restricted, small sample from a single locality south of Phoenix, Maricopa County, Arizona, is presented.


Karyotypes of C. laredoensis, C. gularis and C. sexlineatus from Texas are presented and compared, and the data are consistent with the hypothesis that the latter two are indeed the parental species.


Tongue-flick values are given for Cnemidophorus exsanguis, C. tesselatus and C. tigris. The combined value for the Teiids is significantly higher than any of the other lizard families studied. It is suggested that this correlates with a lack of development of visual communication in this family and importance of the tongue-Jacobson's Organ system in feeding behavior and other types of communication.


Cnemidophorus tessellatus (= C. tigris) collected in August and September in Pinal County, Arizona, had cloacal body temperatures of 41.3±.24°C. at air and substrate temperatures of 33.6±.43°C. and 41.3±1.07°C., respectively. This body temperature approximates that of a rodent of similar bulk, and this lizard is as active and probably remains seasonally as active as a mammal with similar hibernation needs.

Laboratory studies show that lizards when disturbed emit a short, monosyllabic squeak that can be heard by the teiid ear. A sonagram is presented.


Field and laboratory data are presented for Cnemidophorus gularis gularis, C. inornatus and C. uniparens. Mean body temperatures measured in the field were not significantly different between species; however, C. uniparens had the highest value yet was collected under the coldest field conditions. C. inornatus had the intermediate value yet was collected under the hottest field conditions. C. gularis had the lowest value yet was collected under hotter field conditions than C. uniparens. Mean body temperatures measured in artificial thermal gradients were not significantly different between species; C. uniparens > C. gularis > C. inornatus. Thermoregulatory behavior is described and heating and cooling rates given for each species. Lizards heat faster than they cool. Precise control of body temperature is achieved by shuttling back and forth from warm to cool areas in the thermal gradients. C. uniparens is significantly more precise than the other two species; this implies that it spends more time thermoregulating. Behavior is shown to be very important in thermoregulation. Field studies of thermoregulation are suggested.


Laboratory studies of lizards from Oklahoma show that rank is closely related to body weight and aggressiveness. High-ranking males readily tried to mate with females whereas low-ranking males did not; this behavior was directly proportional to testicular condition. Feeding behavior and nutritive condition were not related to rank; adrenal volume was inversely proportional to rank. The significance of these finding to individual fitness in wild populations requires further study.


The breeding season begins in late May; testes are hypertrophic
and sperm production and fat body depletion commences. Adrenal gland volume increases to reach a maximum during the summer, which initiates intraspecific aggressive and sexual behavior. The breeding season ends in late July with opposite responses of the above attributes.


Lizards were collected in late August from El Paso County, Texas. Females had a larger mean fat body weight. Fat bodies contained the highest percentage of lipids (66-97), while liver and carcass ranges were 10-48 and 2-14, respectively. A list of fatty acids identified (8 total) is given.


Analyses of mitochondrial DNA's (which are inherited maternally) and their endonuclease digestion products confirm the hybrid origins of Cnemidophorus neomexicanus and diploid C. tesselatus. C. tigris marmoratus is indicated as the maternal parent species in both cases. The data imply that these two parthenospecies are younger than some races of Cnemidophorus tigris.


G- and C-banding of both meiosis and mitosis in Cnemidophorus tigris show that the X and Y chromosomes are homologous but do not cross over in the centromere region, where they differ in centric position and heterochromatin.


Cnemidophorus tigris populations were markedly depressed in grazed areas in contrast to ungrazed ones. Both lizard numbers and lizard biomass were down in ORV use areas compared to non-ORV use areas.

Seasonal activity, growth rates and movement patterns of a population in Oklahoma were noted. Behavioral observations were made and it was concluded that the population was a stable one with little immigration or emigration.


Laboratory and field observations were made on a population in Oklahoma. Lizards were not territorial, but formed social hierarchies. Aggressive behavior is described. 1 or 2 lizards established themselves as dominants in groups formed in the laboratory. Males were usually dominant over females; the smallest lizards were the most subordinate. Dominant lizards were more active over longer periods of time in both the lab and the field. This may serve to regulate population densities, dominant individuals assuring themselves of an adequate food supply by driving subordinate individuals to less favorable habitats.


Egg-laying behavior, clutch size and incubation times are given for Cnemidophorus sexlineatus viridis.


Sexual and agonistic behaviors of both free-ranging and enclosed populations of Cnemidophorus sexlineatus are described in detail. This species is non-territorial but establishes and maintains social hierarchies. This behavior is seen as the result of the species occupying an essentially two-dimensional habitat.


Observations on individuals of both species excavated from burrows in Albuquerque are given, along with climatological data.

The only piece of information not contained in the following report is the tendency of individuals of both species to seek refuge in a particular burrow even if they have "to run through a gauntlet of collectors" to get there. This implies that lizards are highly sedentary, that individuals are resident in a particular area. There is no indication of intraspecific territoriality in either species, however.


Cnemidophorus inornatus inhabits primarily undisturbed desert grasslands in the Albuquerque region whereas C. neomexicanus is found chiefly in disturbed areas, often man-related, and is able to survive under nearly metropolitan conditions. The two species are reproductively isolated by their habitat preferences, reinforced by the aggressive nature of C. neomexicanus towards C. inornatus. The two species manifest similar seasonal activities. C. inornatus males are more active early in the year and females are more active late in the year. Adults of both species cease surface activity by the third week in September and juveniles by the first week of October. Lizards emerge from hibernation in mid-April; juveniles are more active than adults for a few weeks in spring and before hibernation begins in the fall. The male reproductive cycle of C. inornatus is described. Maximum testicular size is achieved in April and maximum sperm production occurs in May through the first week of June. Minimum testicular size occurs in late July-early August and growth occurs throughout the winter. The fat body cycle is approximately the reverse. The female reproductive cycle is nearly identical for both species. Follicular enlargement of up to 3 per lizard begins in April-May, the first ovulations occur in the last week of May through the first week of June, and eggs are laid from the first week of June through the third week of July (peaks in mid-June). Approximately 25% of the females of both species lay a second clutch. The mean clutch size for both species is 2.13, but ovarian follicles and oviducal eggs are considerably larger in C. neomexicanus. The first hatchlings appear in the last two weeks of July, and new hatchlings continue to appear until the first week of September. Individuals of both species can live for 4 calendar years; 25% possibly live for 5. Individuals are not reproductively mature until their 3rd calendar year. C. neomexicanus populations possess double the reproductive potential of C. inornatus populations by virtue of parthenogenesis; it is suggested that the viability of eggs of the former species is only 1/2 that of the latter, although no evidence for this exists in this situation. The displacement of C. inornatus by C. neomexicanus is
attributed to the aggressive nature of the latter, its preference for disturbed habitats (which are increasing), and its ability to reproduce in areas where the food supply cannot support two individual lizards.


The parthenogenetic species (C. neomexicanus) is identical to the normal species (C. inornatus) in both the natural histological changes of the oviduct and those induced by hormones. Lizards were collected in Albuquerque.


A morphologically variant specimen was collected from dense mesquite within the city limits of Carlsbad. It is compared to the 10 known specimens from the state, and to 10 specimens of C. exsanguis selected because of superficial similarity to the variant. It is concluded that the specimen is a good C. gularis.

42. —. and J. E. White. 1971. Habitat preferences of Cnemidophorus inornatus and Cnemidophorus neomexicanus with reference to conditions contributing to their hybridization. COPEIA 1971(2): 357-359.

Habitat preferences for both species within Albuquerque are described. C. inornatus was found almost exclusively in dense grass. C. neomexicanus was found only in sparsely vegetated areas and areas with large herbs and shrubs, and was closely associated with man-made objects such as trash piles, hedgerows, ditches and fences. Areas where preferred microhabitats come into close enough proximity to permit interspecific contact are described. Hybrids from these areas are described.


Morphometric analyses support the contention that the 6 specimens are indeed hybrids. Histology of the gonads and epididymides is described; notable differences between the hybrids and normal males is discussed. Sperm produced by the hybrids appear to be viable; potential gametogenic abnormalities resulting from their incorporation in a zygote
are discussed.


The activity season lasts from April until October in Brazos County. Most females lay 2, some lay 3, clutches per year averaging 3.38 eggs. Females reach reproductive maturity at 1 year of age. Population turnover is essentially annual although some individuals did survive the winter. Home ranges for both sexes were similar and averaged 13099 m². Year to year climatic fluctuations affected population densities, estimated at 15-24 lizards per hectare, and home range sizes.


The origin and evolution of parthenospecies is discussed in a general review article. The species of Cnemidophorus discussed include dixoni, exsanguis, flagellicaudus, neomexicanus, sonorae, tesselatus, uniparens and velox. Problems suggested for study include determination of the egg activation mechanism(s), elucidation of the chromosomal mechanism of sex determination, problems involving gene dosage compensation (as different ploidy levels are involved in Cnemidophorus parthenospecies), the influences of mutation rates on parthenospecies compared to sexual ones, and ecological interactions between parthenoforms and sexual species.


Cnemidophorus exsanguis, C. sonorae and C. tigris from Arizona and New Mexico were raised and crossed in the laboratory. C. exsanguis from Alamogordo represent two distinct karyotypes (= clones) and these are inherited precisely as demonstrated by rearing several generations from each one in the lab. C. sonorae (3N) X C. tigris (1N) produced a viable tetraploid hybrid. The origin of parthenogenetic Cnemidophorus through hybridization and earlier conclusions on the evolution of allopolyploidy in reptiles is confirmed.

This paper reports an X-Y (XY=male, XX=female) sex chromosome mechanism in *Cnemidophorus tigris gracilis* and points out that most species in the genus lack readily recognizable heteromorphic pairs of chromosomes.


A detailed description of laboratory procedures necessary to successfully raise parthenospecies of *Cnemidophorus* through multiple generations is given. *C. exsanguis* was used primarily, and raised through 4 generations. Other species mentioned were *neomexicanus, sonorae, tesselatus* and *velox*, as well as the sexual species *inornatus, sexlineatus*, and *tigris*. The significance of this capability for future biological research is discussed.


Reproductive energetics for *C. inornatus, C. sonorae, C. tigris* and *C. uniparens* from Arizona were estimated from caloric whole body and egg content. Clutch size was larger in unisexual species and in larger species within a reproductive type. Calories/mg. of eggs were not correlated with either body size or reproductive type; differences in clutch volume between species superceded differences in caloric content of eggs per unit weight. Mean calories per egg were higher in large-bodied lizards and in bisexual lizards independent of size. The clutch calories/body calories ratio was significantly higher in unisexual species, and this fact is discussed. Data suggest that the nature of the competitive environment and the degree of genetic similarity among individuals are important evolutionary determinants of the apportionment of energy to reproduction and the compromise between egg size and numbers in whiptail lizards.


Captive *Cnemidophorus tesselatus, C. uniparens* and *C. velox* exhibit behavior patterns remarkably similar to the courtship and copulatory behavior of closely related sexual species. The courted animal was reproductively active in each instance while the courting animal was either reproductively inactive or postovulatory. This behavior may represent a nonfunctional vestige of sexual ancestry or be necessary to
normal ovarian functions by replacing male stimuli.


The pineal organ does not play a role in the endogenous circannual reproductive cycle of this lizard but may be involved in thermoregulation.


Corpora lutea evidently function to control gravidity and shelling in this reptile and a corpus luteum hormone is probably responsible for this control. An undescribed ovulation behavior and its possible hormonal control is also discussed.


The results suggest that the physiology of sexual refractoriness in C. uniparens (collected in Socorro County, NM) is mediated by the neuroendocrine system.


Lizards from Socorro County, New Mexico, were maintained in captivity under either short (10L:14D) or long (14L:10D) photothermal regimes. Some lizards from both groups experienced two consecutive reproductive cycles. This demonstrates the existence of an endogenous circannual rhythm in the reproductive cycle of this species.


Postreproductive Cnemidophorus uniparens maintained under free-running conditions of constant darkness for 7 months became reproductive
at the same time as controls exposed to long photoperiods. This confirms that the refractory period (a pause in reproductive activity commencing in late summer in nature) is under endogenous control.


The reproductive tracts and associated organs were examined in both sexual and parthenogenetic species of Cnemidophorus, including exsanguis, neomexicanus, tesselatus, tigris, uniparens and velox. The fact that 6 of 9 bisexual females had spermatozoa in their reproductive tracts while all 36 of the unisexual females lacked similar evidence of courtship, reasonably excludes gynogenesis, a cryptic male behavior, and differential male and female activity periods as interpretations for the all-female condition, and supports true parthenogenesis as the most probable mechanism. Seminal receptacles were absent in both the bisexual and unisexual lizards examined. Sex ratios reported for natural populations of bisexual species of Cnemidophorus are biased in favor of males. This may explain the lack of seminal receptacles in these species. An excess of males might serve the same function as stored sperm, namely to insure a maximum realization of reproductive potential.


The morphological cycle of the ovaries and oviducts is examined in individuals of Cnemidophorus exsanguis, C. inornatus, C. neomexicanus, C. tesselatus, C. tigris, C. uniparens and C. velox throughout the reproductive period. Ovaries proceed from a regressed state to a point where they are isolated from the coelom by encapsulating oviducts. An intimate association is established between the oocytes and the infundibular oviductal ostia. Photomicrographs are presented.


Live capture methods and captive maintenance techniques for specimens from Arizona and New Mexico are discussed at length. The Bosque del Apache (Socorro Co., NM) population exhibited a mean clutch cycle of 23 days, with a mean number of 3.3 ova per clutch. The reproductive season in nature terminates at the end of July. Chromosomal and cellular behavior associated with egg production is examined in great detail. Parthenogenesis in this species is of the meiotic type. The somatic number of chromosomes is doubled early in oogenesis presumably by a pre-meiotic endoduplication, and the 3N level is restored by 2 subsequent maturation divisions.

The evidence for and against the hybridization theory (hybridization→ diploid unisexuality→ polyploidy) and the spontaneous origin theory (ability to produce unreduced ova is genetically acquired→ diploid unisexuality→ polyploidy) is reviewed. Cuellar is biased in favor of the latter, which states that hybridization does not result directly in parthenogenesis but only favors it through heterosis. The evidence presented actually supports both theories; that is to say, neither theory can be ruled out depending on the individual circumstance. The evidence supports the hybridization theory in Cnemidophorus, in the opinion of this reviewer.


A total of 175 skin grafts were transplanted among 20 individuals belonging to two separate populations of Cnemidophorus uniparens. Only intraclonal (= locality) transplants were done. 99.8% were permanently accepted, which indicates that all individuals of each population may be genetically identical. These results further suggest that large populations or the entire species may consist of one clone derived from a single individual. All allografts done with C. tigris (a sexual species), using the same procedures, are eventually rejected. Histocompatibility genes are discussed and it is suggested that the technique described here could be used to determine actual mutation rates in parthenogenetic clones, provided that mutant individuals exist and can be detected.


This study was conducted to determine more precisely the degree of variation in histogenes within and between populations to understand as nearly as possible the extent of genetic variation throughout the range of a parthenogenetic species, and thus perhaps shed further light on the probable origins of parthenogenesis. C. velox, with a wide geographic range, and C. neomexicanus, with a restricted geographic range, were used. Lizards of the latter species, from 4 separate localities encompassing 160 miles of the species' range, underwent intra- and interlocality skin transplants. 99+% of the grafts were retained, implying that the lizards over this geographic area are genetically identical. Lizards of the former species from 2 localities in Utah, 1 in Colorado, and 2 in New Mexico were subjected to the same procedure. All interlocality grafts were accepted, as well as interlocality grafts between the 2 clones in Utah and the 2 in New Mexico. All interlocality grafts
between clones from different states were rejected, however. This implies that the species has been derived de novo several times, or that a single clone has "speciated" in different parts of its range. This work supports current thought in genetics that environmental and genetic uniformity are correlated.


It is suggested that the weed hypothesis concerning parthenogenesis in Cnemidophorus is correct, but not the claim for distinct habitats for each species within the broad geographic "weed" area, as each such habitat is a local climax formation and not weedy. It is suggested that those parthenospecies for which specific habitats are proposed exhibit distinct riparian-dwelling affinities. Theories and models of obligatory parthenogenesis are reviewed. There are three compelling reasons for believing that parthenogenetic species can only evolve in isolation from the generating bisexuals: hybridization by males of congeneric species would impede clone establishment; competition would impede clone expansion, and present distributions show largely distinct habitats between congeneric unisexual and bisexual species. Hence, it is reasonable to assume that parthenogenesis evolves either at the periphery of the range, or if within the range, in areas periodically devoid of the generating species. It is suggested that parthenogenetic species rely on novel habitats, and that the availability of habitat is the key to success, not the meiotic ability to produce unreduced eggs. The salient feature of the distribution of several species of unisexual Cnemidophorus (exsanguis, neomexicanus, tesselatus, uniparentes and velox) is the tendency to be floodplain dwellers. Range maps of neomexicanus and tesselatus in relation to drainage patterns are presented. These 5 species also occupy climax communities, but usually where bisexual species are absent. C. inornatus, a bisexual species, is an exception; it occurs sympatrically with several unisexuals in disturbed areas. Conversely, the bisexual C. tigris is almost exclusively restricted to adjacent climax communities characterized by sandy soils. In certain localities of southern New Mexico (in the vicinity of Elephant Butte Reservoir and the Rio Grande) it occurs abundantly in mixed mesquite-creosote associations, but is virtually absent from adjacent pure stands of creosote growing in gravelly soils. Edaphic conditions appear to be important.

The significance of disturbed habitats to parthenogenesis in other kinds of animals is reviewed, along with the displacement of bisexual species by unisexuals. Cytogenetic factors are important in the evolution of parthenogenesis. It is suggested that parthenogenesis is more advantageous in non-territorial rather than territorial animals because the latter would expand too slowly to take advantage of discclimax situations. This explains the absence of unisexual species of birds and mammals; they are so vagile that sexual species would recolonize disturbed areas too rapidly for unisexuals to establish themselves. Clone succession is proposed as better-adapted clones replace less-adapted
ones in particular situations. It is suggested that newly-disturbed areas open to either reproductive mode would be occupied by bisexual species until the origin of a parthenogenetic clone, which would then displace the bisexuals due to its higher intrinsic rate of increase. Selection would promote the survival of clones more or less specially adapted to unique communities of perpetually disturbed areas or areas not occupied by bisexual species. Termination of the physical or climatic conditions promoting and maintaining recurrent disclimax ecologies would cause the extinction of the parthenoforms and the reinvasion of climax communities. Assuming that hybridization gave rise directly to parthenogenetic species is cautioned against. The acceptable corollary to this, in the opinion of this reviewer, is that not every hybridization event leads to the establishment of a successful parthenoform (i.e. C. perplexus); the cytogenetic and ecological factors must synergize.


The question of why so many congeneric species of this genus are found together and exactly what their ecological and geographical requirements are remains virtually unanswered. Sympathy among 7 species of Cnemidophorus (exsanguis, inornatus, neomexicanus, tesselatus, tigris, uniparens and velox) is documented and discussed for several localities (mostly in New Mexico), and the first field experiment dealing with competitive interactions between a parthenogenetic and a bisexual species is reported. Short-term habitat alteration and collecting pressures are implicated as factors affecting the interactive demographics of the above species; in some cases the only species involved are parthenogenetic. Collecting can apparently wipe out populations of several of the parthenospecies if sustained and steady over a period of years. The field experiment involved the bisexual species C. tigris and the unisexual species C. uniparens. The former species dominates in mesquite-creosote habitats near Elephant Butte Reservoir whereas the latter occurs in all habitats from the river to the foothills of the San Mateo Mountains. C. tigris is absent from all habitats in the Rio Grande floodplain. The study site is a weedy field between Tamarix and Populus forests which is adjacent to and interdigitates with C. tigris habitat; C. uniparens is dominant here. This species was selectively removed for a period of several days in each of the years 1975, 1976 and 1978. C. tigris failed to invade this habitat although it could do so easily; it was instead repopulated by C. uniparens from the adjacent gallery forests. The mean size of individuals of this species declined as did the number of reproductives, however. Only 3 individual C. tigris were seen, indicating that this species is actively avoiding the riparian zone. The area was visited again in 1979, when this paper was in proof, and the C. uniparens population was identical in density and mean individual size to the previous year. Individuals predominated on the edges of the field rather than the center, indicating invasion from the periphery. 14 different individuals of C. tigris were seen distri-
buted throughout the clearing, indicating an invasion of this species in the absence of a stable population of *C. uniparens*. It is concluded that perhaps direct competition is a critical factor in this situation after all.


Reproductive cycles were monitored in captives for their entire lives. The annual cycle of a short reproductive period followed by a long non-reproductive period persisted indefinitely in 80% of the animals. The cycle was reduced to 5 months in the absence of environmental cues. The number of clutches laid per individual remained relatively constant, suggesting that it, like the reproductive rhythm, is under endogenous control. There is evidence for multiple clutches during the reproductive period in nature, followed by a long refractory period. The refractory periods progressively shorten in captivity until they become indistinguishable from between-clutch intervals, implying environmental control of the refractory period. Sexual behavior between captive individuals of parthenogenetic *Cnemidophorus* reported by Crews and Fitzgerald (1980) is discussed, and evidence suggests that it is abnormal behavior associated with captivity.


Skin grafting and electrophoresis was done to determine the parental species of suspected natural hybrids in *Cnemidophorus*. Six species (exsanguis, inornatus, neomexicanus, tesselatus, tigris and uniparens) were sympatric in an area 40' by 200' dominated by weedy vegetation along the railroad right-of-way 3 miles south of San Antonio, Socorro County, New Mexico. A stable creosotebush community existed on one side of the area and agricultural lands on the other. *C. inornatus* occurred in very high densities in the area as did the unisexual species, resulting in increased chances for hybridization. *C. tigris* was characteristic of the creosote community and rare in the hybrid zone. 50% of the *neomexicanus* exhibited the characteristic bite marks inflicted during copulation in *Cnemidophorus*. The hybrid specimens (2 *inornatus* × uniparens and 3 *inornatus* × *neomexicanus*) were superficially morphologically similar to the unisexual parent but possessed bluish undersides. Known hybrids in the genus are reviewed; 25 are males, 7 are females and 4 were not sexed. Skin grafting is suggested as a technique for determining parental species.

66.  —. and C. Smart. 1977. Analysis of histo-incompatibility in a
natural population of the bisexual whiptail lizard *Cnemidophorus tigris*.

Abrupt and gradual rejections occurred in a graded sequence in lizards from Utah, suggesting that large numbers of genes and/or alleles are responsible for antigenic properties of skin.


The experiments provided a graded sequence of rejection of skin grafts and indicated that the relative degree of antigenicity of a donor was more or less proportional to its immune response. Probable genetic models for rejection are discussed.


6 different pesticides were found in specimens of *Cnemidophorus inornatus*, *C. tesselatus* and *C. tigris* collected within a 30 mile radius of Presidio, Presidio County, Texas. Pesticide concentrations in lizards increased from June through August. Lizard eggs contained up to 5 times the concentration found in the gravid female. 2 more male *C. tesselatus* were collected (3 out of 7 now known come from this area).


Data are given on whole animal and tissue oxygen consumption and activity temperatures for *Cnemidophorus inornatus* and *C. tigris*.


Data are given for *Cnemidophorus inornatus* (10.8 volume %), *C. sacki* (= *sonorae*, 11.6 volume %), and *C. tigris gracilis* (9.6 volume %) from Cochise County, Arizona. Data are related to altitude and active body temperatures, and compared to other lizards and higher vertebrates.

71. Degenhardt, W. G. 1966. A method of counting some diurnal ground lizards of the genera *Holbrookia* and *Cnemidophorus* with results from the
Cnemidophorus tigris marmoratus is among the species discussed. The topography and climate of the area is discussed in detail, along with earlier herpetological investigations. A method of estimating lizard densities by counting active lizards is developed and compared with some poor attempts by the investigator to do the same by live-trapping. Sources of error are discussed. Six study plots were established along an elevational transect and studied for 2 years. A highly significant correlation of lizard numbers with elevation was established. The corollary contributions of vegetation structure, soil, rainfall and temperature to this correlation are discussed. No distinct conclusions seem to actually be reached by the author.


The same area is re-visited and the same methods used in 1968 and 1969 as was done in 1966 by this author. Lizard population density estimates are given for each study quadrat. It is suggested that an increase in vegetation density up to a certain optimum for each lizard species will result in an increase in population density for that species; increases above that vegetation optimum will result in a decrease in lizard population density. Cnemidophorus tigris is shown to prefer relatively open areas and is suggested to outcompete at least one other congeners (septemvittatus).


Twenty protein bands were identified in C. tigris gracilis, C. t. marmoratus, and hybrids between the two; 12 bands were common to both subspecies and 4 were unique to each. F1 and backcross hybrids were found, indicating that hybrids are fertile. The zone of hybridization in SE Arizona-SW New Mexico appears broader than indicated by Zweifel (1962), although this paper supports that one in other respects; is indeed complementary to it.

74. Douglas, C. L. 1966. Amphibians and reptiles of Mesa Verde Na-
The geology, climate and vegetation of the park are characterized. *Cnemidophorus velox* is found mostly at lower elevations along the southern halves of mesas and is locally abundant around the park headquarters. Lizards were gravid in June and hatchlings were first seen at the end of August. The behavior of captives is described. Endoparasites of the species are listed.


*Cnemidophorus inornatus* forages in the litter beneath vegetation. A graphic representation of food items for this species is given; lepidopteran and coleopteran larvae (41%) and coleopteran adults (12%) are the main prey. Competition with *Holbrookia* and *Sceloporus* is avoided by differences in foraging methods and foods eaten.


A detailed analysis is presented; species used include *gularis* and *sexlineatus*.


*C. sacki xanthonotus* (= *C. burti xanthonotus*) is formally named, described and diagnosed. It is known only from the Puerto Blanco and Ajo Mountains, Pima County, Arizona. It occurs in relictual mesic communities, in the juniper-oak-desert edge ecotone in canyons on west slopes. These canyons have narrow rocky walls well-covered with vegetation, and have intermittent water in their bottoms. The south-facing slope of the type-locality possesses typical plants of the Sonoran Desert; the north-facing slope lacks these and instead possesses *Juniperus*, *Berberis*, *Ephedra*, *Agave* and grasses.

Detailed morphologies and ranges are given for Cnemidophorus bur-ti (all subspecies), C. exsanguis (includes flagellicaudus and sonorae), C. gularis, C. inornatus (= inornatus + uniparens), C. perplexus (= neomexicanus), C. sexlineatus and C. velox. The lack of males in exsanguis, perplexus, velox and the western populations of inornatus (= uniparens) is noted.


Data on daily and seasonal activity patterns, food and foraging behavior, intra- and interspecific encounters and reproduction are presented and discussed for C. exsanguis (probably = sonorae) and C. tigris gracilis. The author concludes that present competition between the two is largely potential based on a seeming abundance of termites, a staple food item for both species, despite the fact that the two species occupy almost mutually exclusive habitats on the study area and that varying degrees of difference occur in other ecological factors examined.


Individual lizards dig burrows that parallel the sand surface at a depth of 20 mm, and that are approximately 1.5 times as long as the animal itself. They allow the belly of the lizard contact with damp subsurface sand and the back to remain in contact with the warm dry surface sand. It is suggested that the lizards are behaviorally thermoregulating.


Analysis of the fossil lizard fauna (including Cnemidophorus sexlineatus), all of which are still extant today, indicates a climate of less extreme winter temperatures and generally more arid conditions than today during the Sangamon interglacial.

A comprehensive review of the literature on this species is presented. This species belongs to a genus that primarily inhabits deserts or other arid regions. It penetrates far to the north and east of its congeners in the United States, into a region which under original conditions was chiefly deciduous forest. It exists partly in disjunct populations selecting mainly xerothermal habitats such as beaches, sand dunes and the edges of cultivated fields. It seems to require open areas wherever it lives. The species is abundant in the sandy floodplain of the Kansas River. A flood in July of 1951 inundated the area and destroyed the population, which did not recover its former numbers for several years. A population was studied for a period of 9 years on the University of Kansas Natural History Reservation. Deeply eroded gullies in fallow fields, heavily grazed pastures and exposed rock and soil of a limestone quarry provided excellent habitats and lizards were numerous at the beginning of the study. Vegetational succession proceeded as the area was protected and the population declined as open habitats were reduced. The study was terminated when lizards became few in number and no significant new data was being accumulated. Seasonal activity began in April, peaked in June, then abruptly fell off from July through September. Daily activity was bimodal in hot weather. Individual active body temperatures ranged from 38 to 42°C; lizards will tolerate 5° below and 2° above this range before seeking shelter. Air temperatures were always below active body temperatures. This was the last species of reptile to emerge from hibernation on the study area. An individual male had an observed home range of .31 acres although this figure is probably biased because the habitat was not uniform; female home ranges were slightly smaller. Activity was concentrated in particular parts of individual home ranges. Lizards were observed to make extremely long movements and shift home ranges during drought years, when vegetation decreased and more habitat became suitable. Lizards dig burrows extensively in soil and beneath rocks when they cannot use those abandoned by other animals. Burrows are defended. Vegetation is also used in which to seek temporary refuge. Food habits from other parts of the species range are discussed; it is noted that olfaction plays a major role with lizards frequently digging for prey such as insect larvae. Copulatory behavior is described; mating appears to be aggressive and promiscuous. There is sexual dimorphism in body proportions and color. The sex ratio is 1:1. Gravid females were first recorded late in May and recorded latest in mid-August. Two clutches per year are probably laid; females mature sexually and lay eggs during their first year of life. Clutches range from 1-6 eggs; first-year females average 2.0 eggs/clutch while older females average 4.4. The earliest hatchlings emerge during the first 2 weeks of August and the second clutch hatches during September. Hatchlings average 32-35 mm snout-vent length and weigh about one gram. The most successful of them add 20 mm and come to weigh 1/2 of adult weight during the six weeks before hibernation. Over-winter survivors reach adult size by summer's end, although growth rates slow to 1/2 that of hatchlings. The largest lizard measured, 5 years old, was 84 mm SVL. Tail-break frequency increases as lizards age, but even 1/2 of the largest and oldest group retain original tails. No sexual difference is apparent. The ultimate escape tactic is speed; however, lizards rely initially
heavily on crypsis. Several species of snakes, hawks, the Collared Lizard, skunks, the raccoon and armadillo are predators. Almost all lizards were infected by the chigger Trombicula alfredugesi. The population near the reservation headquarters varied from 40 to 72 lizards per acre over a 4 year period; combined percentages of first through sixth year individuals in that population were 57, 25.4, 10, 5.4, 1.5 and 0.7. Loss of roughly one-half of the individuals in each age group in the course of a year is indicated.


This is mostly a review article and presents data on Cnemidophorus exsanguis, C. sexlineatus, C. tesselatus, C. tigris and C. velox. Original data are presented concerning age-size class distributions and reproductive status of a population of C. tigris marmoratus from Reeves County, Texas. Males are larger than females, females may reproduce when one year old, and the smallest reproductive female was 75 mm SVL.


The lipid cycles in carcass, liver and post-coelomic fat bodies were determined for adults of both sexes of lizards collected near the NE city limits of El Paso, Texas. Fat bodies were used for maintenance during winter dormancy. The timing of reconstitution of lipid reserves during the active season differed between the sexes in correlation with their reproductive roles. Variation in activity between the sexes during the active season is indicated.


The topography, geologic history, climate, vegetation, and recent environmental changes occurring in the region are discussed in detail. Cnemidophorus velox occurs in the region; historical accounts and the nomenclatural history of the species are New Mexico is discussed. Data on morphological variation is discussed; possible males or hybrids with C. inornatus are described. C. velox occurs between 6000 to 8000 feet and is most common at about 6400 feet. It prefers open areas of the Roughlands life belt especially where saltbush-sage associations occur in isolated patches in pinyon-juniper savanna. Notes on reproduction are given.

The vegetational basis of biome patterns in the Guadalupe Mountains ecosystem is described. The relationship between biomes and lizard species distribution in both grazed and ungrazed habitats is explored. Cnemidophorus exsanguis is characteristic of the relatively mesic margins between deciduous and evergreen woodlands on canyon slopes at elevations around 5500 ft. C. inornatus is characteristic of xeric shrub desert flats at 4000 ft. C. tesselatus is abundant in the more mesic succulent desert and on canyon slopes at about 4700 ft. C. gularis and C. tigris are scarce; the former occurs in grassland remnants and the latter in arenaceous areas of shrub desert. C. tesselatus is abundant throughout the temporal sequence of revegetation of a pipeline construction scar in the succulent desert biome, whereas it declines in grazed habitats versus protected ones in this biome. There are no differences in C. exsanguis populations between grazed and ungrazed habitats in evergreen woodland. Evidence indicates that C. tigris and C. septemvittatus replace each other from shrub desert through succulent desert transitions in the Big Bend region of Texas, and therefore, by implication, C. tesselatus does not compete successfully with either and is relegated to marginal habitats (i.e. canyons, which can be considered disturbed areas).


Cnemidophorus sonorae and C. tigris gracilis were among the species studied on the Santa Rita Experimental Range in Pima County, Arizona. Desert grasslands in the southwestern United States have been invaded by mesquite during the last 100 years. C. tigris populations were significantly lower in mesquite-free habitats versus undisturbed mesquite and mesquite with clearings. C. sonorae populations were significantly higher in mesquite-free and mesquite with clearings habitats than in undisturbed mesquite. There are indications of differential use of the mesquite with clearings habitats by the two species.


Specimens were collected in the Oklahoma panhandle at an elevation of 4400 feet in canyons in pinyon-juniper associations.

Lizards from near Tucson, Pima County, undergo a seasonal cycle in which gonadal size is minimal in September-October. Male reproductive organs gradually recrudesce during the winter months spent underground. After they emerge from hibernation in March-April the testis, seminiferous epithelial height and tubule diameter gradually increase in size through April and May, reaching maximum size in June-July followed by rapid regression in August. Mating is first observed in the field in May. The ovaries undergo a period of heavy yolk deposition from early April to May, and remain functional until August. A thick circumtesticular subtunic layer of equivalent interstitial material (Leydig cells) is reported and described for the genus.


Teiids have undergone an extensive adaptive radiation. There are about 40 living genera with a total of some 175 species. If chromosome data alone were used, one would definitely consider the family to be of South American origin. The fossil record shows that such an interpretation is unwarranted. There was a rich and diverse macroteiids fauna during the Cretaceous in North America with all modern lineages represented. Teiid diversity appears to have dropped drastically in North America following the Cretaceous, for the only positive identifications are of Cnemidophorus-like species. Thus the present distribution of the Teiidae is one of range shift or contraction. It is possible that the loss of climatic equability toward the end of the Cretaceous, postulated to account for dinosaur extinction, eliminated from North America all teiids that were not adapted to xeric conditions. Absence of a Cenozoic land bridge until the Pliocene slowed recolonization of North America by South American teiids. Although Cnemidophorus-like lizards have been in North America from at least the early Miocene, they have not been the source of a major adaptive radiation. This may not be due to lack of time, but to the rigid specialization of Cnemidophorus to an open niche with high insolation.


A fenced population that had been irradiated for 10 years was studied, as was a fenced non-irradiated and a free-ranging population.
No significant differences in allele frequency were found at 26 allozyme loci examined. This is the most polymorphic and heterozygous of the 21 lizard species so far examined (35%; mainland species only). A general trend is apparent. Fossorial lizards have uniformly low levels of heterozygosity (ca. 1%), territorial "sit and wait" predators are intermediate (ca. 5%), and highly vagile apparently nonterritorial species are most heterozygous (ca. 10%). If this trend is of biological significance, it can be explained by (1) the niche width variation hypothesis which predicts higher variability in populations where individuals are exposed to large-scale environmental heterogeneity (in reality, comparison of "niche widths" among the diverse lizards used in this study is difficult at best, and no data is available), and/or (2) the population size or gene flow variation hypothesis, which predicts that, all other things being equal, vagility would tend to increase the effective population size by reducing inbreeding, which would promote higher levels of genetic variation.


The parietal eye is important for reproductive synchronization and thermoregulation in lizards. There is a general trend of low-latitude restriction of parietal-eyeless lizards. The Teiidae are parietal-eyeless and centered on the equator where 18 of the 31 genera overlap. The genus Cnemidophorus ranges northward to 43° latitude (it is interesting to note that many of the northernmost species are parthenogenetic).


The amounts and fatty acid composition of the main lipid classes for pre- and post-ovulatory oocytes of lizards from Graham County, Arizona, were determined and discussed in relation to thermal regime, mode of reproduction, and diet.


Cnemidophorus tessellatus is among the species used in a general account of the variation in gross structure that occurs within and between lizard families. 4 groupings based on this variation are discernable; C. tessellatus is somewhat intermediate between the Lacertid and Gekkonid clusters.
Laboratory, field and artificial enclosure observations were made on a population inhabiting a sparsely vegetated sand dune habitat in the floodplain of the Kansas River. Thermoregulatory behavior is described. The preferred body temperature is 40–41°C., the thermal activity range is 34–41°C., lizards will not become active until their body temperature is approximately 20°C. There are different thermal thresholds for different behaviors. Daily activity cycles are described, with the hunger drive implicated as the initiating factor. Seemingly stereotyped defecation behavior is described. Peak seasonal activity occurs in May and June; by the beginning of September adults are only occasionally active. This is correlated with an increase in body fat storage and concomitant increase in the daily thermal threshold for activity due to a decrease in the physiological need for food. Egg deposition sites are typically open, sloping, fine-grained sandy areas. The population exhibits 4 distinct egg-laying periods, each representing a different age-size class of females. Females 3 years or older probably lay 2 clutches per year. Clutch size for yearlings is 1–3 eggs and for older females is 3–5 eggs. Incubation averages 50 days. 4 types of shelter (3 of them burrows) and the behavior associated with making and/or using them are described. Both vision and olfaction are used in hunting; associated behaviors are described. There are sexual, size, and seasonal differences in types of prey taken. Food habits are analyzed in detail. Predators and parasites are briefly discussed. Straight-line social hierarchies are established under captive conditions. Color is only functional in threat behavior between aggressive males. Mating behavior is described. Aggressive behavior in nature is thought to achieve population spacing in favorable habitats; less aggressive individuals being displaced to suboptimal habitats.


Serial histological sections of the complete urogenital systems of 9 F_2 specimens belonging to two ontogenetic series of Cnemidophorus sexlineatus raised in captivity in isolation from males were examined, as well as that of the F_1 mother of one of these series. No evidence of spermatozoa or testicular tissue was found. Comparative material reveals that the histology of the urogenital tract is similar to that of females of the bisexual species C. sexlineatus and C. tigris. Evidence of 8 specific points useful in the determination of true parthenogenesis (absence of males, morphological variation, ploidy levels, histocompatibility, histology of the reproductive tract, oogenesis, reproduction in captivity, and karyotype inheritance) is reviewed for C. sexlineatus. It is concluded that this species is parthenogenetic and that normal reproduction does not involve sex-reversal, self-fertilization,
gynogenesis, hybridogenesis, or spermatozoa in any way whatsoever.


Grassland habitat of the present type was absent during the last major Pleistocene pluvial. Animals associated with it had to invade through habitat corridors to the northwest or from relatively low-lying areas along the Continental Divide to the southeast. Climatic and vegetational changes of the area since the last major pluvial (Wisconsin) are discussed in detail. Cnemidophorus tigris septentrionalis is found along washes and in rocky areas of pinyon-juniper habitats in the study area. C. tigris marmoratus is found in the Rio Grande basin to the east and southeast, and the two subspecies are separated by the Continental Divide. Previous contact was impossible and the former invaded from the north and northwest. Cnemidophorus inornatus is rare in the study area; it occurs in a few localities bordering Gallegos Canyon and at the borders of sagebrush and grassland habitats. Only clinal variation exists between this isolated population and those in the Rio Grande basin, therefore they were probably contiguous at one time. The present population invaded during the post-pluvial period, when the climate was most likely warm and wet rather than warm and dry, and may have been isolated for a maximum of 4000 years.


The fauna includes Cnemidophorus perplexus. No age is given for the material, nor is it clear which of the currently recognized species is referred to.


Cnemidophorus tigris septentrionalis is common in greasewood, cottonwood, tamarisk and willow floodplain habitats with sandy to clay soils in southeastern Utah. It is common over a wider range from barren desert washes to pinyon-juniper habitats with gravelly to rocky soils at Arches National Monument, where C. velox overlaps slightly with it, extending throughout the elevational range of pinyon-juniper habitat. There are local habitat variations for both species apparent throughout the region. C. velox is restricted to the Colorado Plateau Province; C. tigris septentrionalis occurs in that plus the Uinta Moun-
Scutellation and various aspects of color pattern are analyzed by univariate and multivariate statistical techniques for populations from the complete geographic extent of the range of this species in the area of interest. A remarkably complete review of the literature on this species is provided. This study confirms the ecological characteristics documented for this species. *C. tigris* is never found in habitats with dense grass or shrubs, or on inclines exceeding 30°, and rarely on those exceeding 15°. It is also unusual to find *C. tigris* in areas not dominated by creosote; where it is found elsewhere, the species frequents mesquite hummocks in sandy terrain. Creosote communities occupied are usually on gravelly to rocky well-drained terrain such as alluvial fans. It is never found at elevations exceeding 5000 feet and is fairly uncommon above 4000 feet. The range of *C. tigris* is consequently somewhat disjunct in the Basin and Range topographic province; maps are provided of both. Three new subspecies are named; diagnoses, descriptions and photographs of the types are provided. One, *C. t. reticulariens*, occurs in the Pecos River drainage of New Mexico as well as parts of west Texas and Mexico. *C. t. marmoratus* occurs in the Rio Grande drainage of New Mexico, the Tularosa Basin and westward to the Continental Divide, as well as into west Texas and parts of adjacent Mexico. These two subspecies belong to the same species cluster. It is believed that the subspecies provide geographically and taxonomically identifiable entities while the species clusters more realistically indicate units of evolution. Glacial and interglacial sequences during Pleistocene time are discussed as the most probable cause for the fractionation and differentiation of *C. tigris* east of the Continental Divide today. Some quite tentative inferences about predation and population structure are drawn based upon the museum specimens examined for this study. The latter do, however, conform to what has been previously suggested by other workers. There is not a bimodal pattern of emergence of hatchlings as could be inferred from previous field work—that is, hatchlings begin to appear, a single numbers peak is achieved and then emergence falls off.

101. Holland, R. L. 1965. A comparative study of morphology and plasma proteins of the blood in the lizard species *Cnemidophorus tes-
selatus* (Say) (Reptilia: Teiidae) from Colorado and New Mexico. M.A. THESIS, UNIVERSITY OF COLORADO. 116 p.

Electrophoresis of plasma and erythrocyte proteins were performed on lizards from 3 populations: near Pueblo, Pueblo Co. and on the Purgatoire River, Las Animas Co., Colorado, and near Caballo Dam, Sierra
Co., New Mexico. The latter population differs significantly in the relative proportions of two of the four major plasma protein groups found in this species. Morphological comparisons are made; color and pattern also differ significantly. Color photographs of specimens are provided. Statistically significant differences are also found in several scale characters. Nomenclature is discussed, and the type locality is restricted to "the junction of the Arkansas River and Fountain Creek", Pueblo Co., Colorado. A 100-mile gap exists at the time of this study between Colorado-Oklahoma and New Mexico-Texas populations; morphological differences are felt to be taxonomically significant. It is suggested that the distribution of C. tesselatus is uniformly riparian, reflecting routes of dispersal. It is further suggested that the current distribution map implies that the species is less widespread than it once was, the range discontinuities reflect withdrawal from previously occupied areas. Current relictual populations, if indeed that is what they are, further imply a measure of ecological/evolutionary age for this parthenospecies (opinion of this reviewer).

C. tesselatus can be found in a variety of microhabitats, but are never far removed from some drainage system, however ephemeral. Low shrubby vegetation and few trees characterize habitats. The species seems to prefer sandy-to-silty soils, and not extremely rocky nor grassy areas. The species is sympatric with C. sexlineatus in Colorado and with C. inornatus and C. tigris in New Mexico. Colorado lizards can be approached within 2-3 feet; they can be followed for extensive periods of time and will approach a lizard noose out of curiosity. New Mexico lizards are extremely wary and cannot be approached any closer than 10 feet. The literature is reviewed and the conclusion reached that, on the basis of morphology, there is no indication that unisexual species are more or less variable than bisexual ones. It is suggested that the different morphological characters reported here represent independent genetic factors and that differences between the 2 areas reflects a pattern induced by natural selection. It is further suggested that northern populations of C. tesselatus are distinct from southern ones and perhaps worthy of subspecific rank, which is not proposed at this time because of the preliminary nature of this work.


The fauna includes Cnemidophorus sexlineatus, and notes on climatic change from maritime to semiarid are given.


A population was studied over a period of 2 years from late May through the end of August at a site approximately 2 miles west of the
New Mexico-Arizona border along the Portal Road, Cochise County, Arizona. A pitfall trap grid covering one hectare was established. The site was at an elevation of 1500 m., with sandy soil and a few scattered rocks, dissected by numerous shallow, poorly defined washes. Prosopis and Ephedra were the dominant plants, with Acacia, Flourensia, Gutierrezia and Bouteloua. Plant cover was 15-20%, increasing to 30-35% after summer rains. Heteromyid rodent mounds and burrows were numerous and a major source of shelter. Eight other lizard species were sympatric, none of them congeneric. Daily activity was bimodal; 75% of captures occurred between sunrise and 1130 hours with the remainder occurring between 1730 and 1930 hours. This pattern broke down on cloudy days. Rainfall depressed activity for as much as 24-36 hours after heavy rains (more than 3 cm). Seasonal activity peaked the first year during the second half of June with an average of 17 lizards per day handled, and declined to 3.5 lizards per day handled during the second half of August. Seasonal activity was steady throughout the second year, ranging from an average of 2.5 to 4.5 lizards handled per day. Roadrunners, burrowing owls and loggerhead shrikes were observed to prey successfully on C. unipares; remains were found in the stomach of Crotaphytus wisiienii. Potential predators are discussed. Tail-break frequency increases in older age classes; the overall percentage is 15.6, which is low compared to C. tigris. This is possibly due to a higher success to attack ratio for C. unipares predators and differences in life-spans between the two species. Mature females range from 58 to 77 mm in snout-vent length (mean SVL is 65.5±3.9 mm). All lizards are reproductive by early June; reproduction continues through the first half of July, then rapidly drops off and ceases by early August. Clutch size ranges from 1-4 with a mean value of 2.77±.06. There is a significant positive correlation between clutch size and SVL. Two, possibly three clutches are produced annually; clutch intervals varied from 21 to 28 days. No significant correlation existed between SVL and egg size or egg weight. The total clutch weight/body weight ratio ranged between 9.6-20.0 (mean 14.4±.24). Forty-seven lizards had home ranges entirely within the study area; home range size was not correlated with either the number of recaptures or SVL. Mean home range size differed highly significantly between the two years. The mean home range size was 815±88 m² (range 120-2386) for the first year and 417±62 m² (range 240-746) for the second based on 39 and 8 lizards, respectively. Normal rainfall preceded the first study season whereas the second was preceded by very heavy precipitation, which greatly increased the production of desert annuals and their invertebrate herbivores. Apparently C. unipares responded to increased prey availability by reducing the average home range size. No territoriality nor aggressive behavior was observed; lizards forage, seek shelter, and fall into the same pitfall traps without paying the slightest overt attention to each other. Growth rates remained the same over the entire study period; differences in prey availability did not influence the volume of prey consumed. Growth rates were negatively correlated with SVL. A sharp decline in growth rate occurs with the attainment of reproductive maturity. Density estimates of adult lizards for the 2 years were 103±6 and 78±12 per hectare; the total number of lizards marked was 135 and 138 and the number of different individuals recaptured was 98 and 82,
respectively. Hatchlings achieve reproductive maturity the season following birth. Less than 10% of the population consisted of the larger size classes in late May, strongly suggesting annual turnover of the population. Only 12 of the 133 lizards marked during the first year were recaptured the second year and, although some migration and shifting of home ranges occurred, this should have little effect on age-size class proportions of the population.


The following species of Cnemidophorus lack internal pigment: grahami (= tesselatus), perplexus (= neomexicanus or inornatus), sacki (= gularis or exsanguis), sexlineatus and tesselatus (= tigris). The significance of this fact in light of their ecological aspects is briefly discussed.


Life belts and vegetation associations of the region are described. Cnemidophorus perplexus (= inornatus) reaches its highest abundance on sandy alluvial fans with scattered areas of small rock in the catclaw-tobosa association. It also occurs in nearby sandy areas of the Plains life belt. Cnemidophorus grahamii (= tesselatus) reaches its peak abundance in the creosotebush-catclaw-blackbrush association adjacent to the mountains. This area is quite rocky with little grass but many desert shrubs under which rodent burrows are common. This species also occurs at rocky mouths of canyons, on rocky canyon bottoms and their associated slopes, and in sandy areas (salt cedar-mesquite and creosotebush associations) of the Rio Grande Basin to the west. Cnemidophorus gularis octolinearis (= exsanguis and gularis) occurred in rocky areas of the mountains and plains in several vegetation associations (the authors were unknowingly dealing with both species here). Cnemidophorus tigris was not found in the study area but occurred in the Rio Grande Basin almost exclusively in the catclaw-creosotebush association.


Comparisons were made between heavily and lightly-grazed chaparral, desert grassland, mixed riparian scrub, cottonwood-willow and Sonoran desertscrub habitats. The abundance and diversity of lizard spe-
cies were down in all heavily grazed habitats except Sonoran desert-scrub. Cnemidophorus exsanguis (= probably flagellicaudus) and C. velox were totally extirpated in some cases and Cnemidophorus tigris numbers drastically reduced due to the elimination of favorable microhabitats and/or the reduction of food supplies.


Specimens of Cnemidophorus velox from Colorado and C. inornatus, C. tesselatus, C. tigris and C. uniparens from New Mexico all possessed 2 germinal beds (GB) per ovary. These are compact and located on the dorsal ovarian surface antero-posterior to each other. Each ovary of the above species undergoes 1-3 ovulations (presumably per year) except for C. tigris, which ranges 1-4. Instantaneous fecundity (the number of ovulations from both ovaries at one time) is inversely proportional to rates of follicular atresia in preovulatory ovaries of lizard species with 2 GB/ovary. Temperate species tend to have relatively higher instantaneous fecundities than tropical species, which also tend to have only 1 GB/ovary. All the species of Cnemidophorus examined, however, have relatively low instantaneous fecundities for their GB count and latitudinal position. This would tend to substantiate the fact the Teiidae are by and large a tropical family and that the genus Cnemidophorus has expanded into temperate regions, and also that reproductive strategies may be evolutionarily stable, complex, and inert (this reviewer).


Home ranges estimated for male, female, and juvenile C. tigris in Nevada are .18, .10 and .09 acres with the minimum polygon method and .71, 1.28 and .54 acres with the density probability function. Factors influencing the estimation of home ranges are discussed.


Individuals of Cnemidophorus inornatus and C. tigris near Las Cruces, New Mexico, were followed for their entire daily activity period. The former species spent more time behaviorally thermoregulating and foraged more thoroughly over a smaller area than did the latter.

Previously published data on several species of Cnemidophorus (exsanguis, flagellicaudus, inornatus, neomexicanus, tesselatus, tigris and uniparents) are taken to show that variation in several scale counts is much greater in bisexual than parthenogenetic species.


Cnemidophorus tesselatus is most abundant in Colorado in arroyos, gullies, and hillsides adjacent to or along river bottoms. It generally occurs in abundance locally when and where found, although it may be absent from equally suitable habitat only a few miles away. The area of this particular study is a 2.03 acre site located on bluffs above the Huerfano River in Pueblo County, Colorado, 26.2 mi. SE of Pueblo at an elevation of 5000 feet. It is heavily overgrazed with scant vegetation, and with several man-made topographic features. The summers are hot and the winters generally rigorous. Dominant vegetation consists of Chrysothamnus nauseosus, Opuntia polyacantha, O. arborescens, Sal-sola pestifer and Yucca glauca. Lizards were captured by noosing, and drift-fence trapping and permanently marked. Resident lizard behavior varied from fleeing after being noosed once to being noosed 20 or more times with little or no escape reaction upon approach by the nooser. Lizards were seldom trapped more than twice, however, before they "learned" to avoid them. All residents were eventually marked. Lizards were considered hatchlings, juveniles, subadults or adults if they were 39-48, 49-66, 67-80, and greater than 80 mm snout-vent length (SVL), respectively. Data for this study is based primarily on the period 18 May-10 September 1965. 87 lizards (16 juvenile, 17 subadult and 54 adult) were marked between late May and mid-July. 17% were never recaptured; the others were recaptured 1-30 times. 35 hatchlings were captured during the fall. The reproductive cycle is discussed in detail. A single clutch of 1-4 eggs was laid during 1965; larger lizards had larger clutches. Oviducal eggs are retained from 3 days to a week or longer; eggs retained longest require a shorter incubation period. Oviducal eggs were first found 12 June and last found 23 July. Evidence suggests that 2 clutches were produced in 1965; 1964 was one of the driest and 1965 one of the wettest years ever recorded in the Pueblo region. Rapid accumulation of large fat reserves begins after oviposition; most older lizards disappeared by mid-August. There were two peak periods of egg-laying, centered around 20 June and 8 July. The first period involved primarily the oldest and largest members of the population. Adults remain in the underground nests for at least 2
days after oviposition. Nest sites were selected in substrate permitting easy burrowing, frequently on a well-drained slope with sufficient soil moisture to insure successful incubation. These slopes were typically devoid of vegetation and exposed to unrestricted solar radiation at all times of the day. Gravid females intent on nesting behave quite differently from non-nesting individuals and these behavioral differences are readily distinguishable. This behavior is best characterized by extended movements out of the home range, scouting of unfamiliar terrain, intensive chemoreception and extreme wariness. Observations indicate that females compete for and "parasitize" the nest sites of one another. Nest sites are defended prior to and immediately after oviposition. Nest sites are communal and females will return periodically over 3 days to scratch additional debris about the nest. It is suggested that lizards return to nest in the same area from which they hatched. Burrows and burrowing behavior is described. Reproductive success was significantly higher in 1965 than 1964. Incubation time varies from 60 to 74 days; the most important variable the length of retention of oviducal eggs. It is suggested that older females retain eggs longer because they are more adept at selection and preparation of nest sites, implying ontogenetic learning. Nest temperatures fluctuated daily between 20-34°C. The first hatchlings in 1965 appeared during the second week of September, although normally they appear two weeks earlier. They remain adjacent to the nest and use it for an overnight shelter after hatching. Many may use it as a hibernaculum as many are caught in the same spot the next spring. Hatchlings continued to emerge until October 5, leading to different size classes which are maintained throughout adulthood. Reproductive maturity is reached during their 3rd growing season (approximately 22 months). Growth rates decline sharply when subadult size is reached; rates are intimately associated with annual environmental productivity. Hatchlings vary between 39.1 mm and 48.2 mm SVL and 1.4 gm to 2.9 gm. Body temperatures between 34-42.6°C. (mean 39.3°C.) were recorded for active lizards. Spring emergence occurs from mid- to late April when soil temperatures to which lizards are exposed reach at least 15°C., fat reserves become depleted and the hunger drive activated. Adults disappear by mid-August although activity continues through mid-October. Hibernacula are all located on SE-facing slopes completely devoid of vegetation and exposed to full solar radiation. The smallest lizards are the first and the largest last to appear in the spring. Daily activity usually begins between 8 and 10 a.m.; the greatest amount of activity occurs between 10 a.m. and 1 p.m. Subtle shifts in this pattern occur during the active season.

Daily recapture rates average 15-20% of the resident population; a maximum of 34% was recorded on August 2nd. All members of the population are not active each day, even though optimum conditions may prevail. Failure to emerge is attributed primarily to success in obtaining food. Different kinds of burrows are dug and utilized for different purposes; an individual lizard may dig several and use them all over the course of a season. All burrows are exclusive and vigorously defended against intrusion by non-residents. Other types of social interaction do not occur. Home ranges are maintained, but are not mutually exclusive and overlap broadly. Sizes for three were .16, .21 and
.25 acres. Migration, except during the nesting season, is minimal; immigration and emigration are negligible. Adults move the least, subadults the most. A population density of 40/acre on the study site was measured during July, with a density of 10/acre in less favorable habitat surrounding it. The population consisted of 19.5% juveniles, 19.5% subadults (2 years old), 34.5% intermediate adults (3 years) and 26.4% old adults (4 years or more). Annual replacement is probably less than 20%. Masticophis flagellum is a constant and troublesome predator; other potential predators include the snakes Pituophis, Hypsiglena, Crotalus viridis, Thamnophis cyrtopsis, the lizard Crotaphytus collaris (rare on the study site), and roadrunners. Of the 35 hatchlings marked in 1965, only 1/2 were recaptured in 1966.


A list of stomach contents in 219 stomachs of Cnemidophorus tigris tigris is given. Almost all insects eaten were injurious to range plants. Orthoptera, Isoptera, Lepidoptera, Diptera and Homoptera were present in greatest frequency; many were larvae or pupae.


Cnemidophorus tigris was one of the species used.


Groups of five conspecific lizards of Cnemidophorus neomexicanus and C. tessellatus (parthenogenetic) and C. sexlineatus (bisexual) were observed in identical outdoor enclosures to determine whether the parthenogens acted more nepotistically towards each other than did the bisexuals as predicted by kin selection theory. Aggressive interactions, competition over food items and fighting were less common in parthenogens than bisexuals, indicating that the genetic relatedness of the former may affect behavioral differences. Genetic unity may also lead to cooperative space use by parthenogenetic lizards, while bisexual whiptails, which are less related to each other, may compete for limited spatial features. Groups of conspecific parthenogens used a significantly greater number of sites for digging burrows than did the more site-specific bisexuals. Neither type maintained territories nor defended objects to the exclusion of conspecifics, and both shared objects under which they burrowed. Parthenogens shared actual burrows 9 times, while this occurred only once among bisexuals. As the number of lizards
above ground increased in each enclosure, aggression levels increased significantly in _C. sexlineatus_ groups containing males. Above ground activity in all species groups peaked in late morning to early afternoon. Nepotistic behavior was never observed among parthenogenetic lizards for several possible reasons. First, members of parthenogenetic populations may not be genetically identical due to independent origin of clones, mutation and/or recombination. Second, because these species are hybrids between two or three bisexual species, they may contain gene combinations that result in competitive rather than cooperative behavior. Third, whiptail species do not defend resources, so opportunities for sharing or sacrificing resources are low (from abstract).


A portion of the preceding study. _C. sexlineatus_ and diploid _C. tesselatus_ used were collected at Conchas Lake State Park, San Miguel Co., New Mexico, triploid _C. tesselatus_ from near Florence, Fremont Co., Colorado, and _C. neomexicanus_ from Albuquerque, Bernalillo Co., New Mexico. Behavior for groups of conspecifics was quantified in outdoor enclosures. Burrows could be dug under 6 objects in an enclosure, along the walls or in open sand. Objects were not equally utilized by any group except female _C. sexlineatus_. _C. tesselatus_ constructed burrows in open sand more frequently than other groups; all the partheno-species used burrows significantly more than the bisexual groups. 59% of all unisexual lizards observed burrowing used 3-6 sites whereas only 4% of all bisexual lizards seen used more than 2. The lack of site-specificity in the parthenogens is related not only to their genetic similarity to conspecifics but also to their propensity for disturbed habitats where environmental fluctuations are constantly destroying burrows. 20% of all _C. tesselatus_ burrowed in open sand, whereas only 6% of the _C. neomexicanus_ and 13% of all _C. sexlineatus_ did. Of the 9 instances of burrow sharing between parthenogens, 8 occurred in _C. tesselatus_ groups (4 2N and 4 3N). Burrow sharing is attributed to tolerance rather than cooperation. Burrow sites were not defended nor were particular objects monopolized or controlled by high-ranking lizards of any species group. No differences between bisexuals and parthenogens were detected in activity parameters measured. _C. neomexicanus_ was more aggressive than _C. tesselatus_, but aggression was highest in groups containing male _C. sexlineatus_. It is concluded that cooperation does not occur between parthenogens, but tolerance for conspecifics is higher than that of bisexuals. The greater incidence of burrow sharing between parthenogens (8 instances in 75 lizards observed versus 1 in 75) is presented as support for kin selection theory. No other variable measured (time of activity, habitat use, defence of resources or aggressive behavior) differed between the species in relation to their reproductive mode.

The population exists in the vicinity of Conchas Lake, San Miguel County, New Mexico. The habitat is described and morphological comparisons made with other populations of the species. It is concluded that this population is the result of man-made introductions.


A belt transect from the mountain crests to the valley floor was censused (T22-23S and R4-5E). The vegetation, soils and topography are described. *Cnemidophorus perplexus* (probably = *neomexicanus*), *C. tessellatus* and *C. tigris* were collected and discussed.


*Cnemidophorus tigris* at Afton and Kilbourne Hole, Dona Ana County, New Mexico, confine themselves generally to the neutral colored islands of sand and mesquite bush desert scattered through the lava fields. Lizards foraging on the lava retreat to these when disturbed.


A description of the range (vegetation, rainfall) and a brief summary of earlier herpetological surveys done in New Mexico are given. *Cnemidophorus perplexus* (= *inornatus*) and *C. tessellatus tessellatus* (= *C. tigris marmoratus*) were collected and briefly discussed.


The name *Cnemidophorus velox* is resurrected for this lizard. The taxonomic history of this species and of others confused with it (i.e. *exsanguis, inornatus*) is discussed. A diagnosis is given. This species typically occurs in woodland and coniferous forest. The type locality

A very brief note on the first known specimens from the state.


*Cnemidophorus sacki* exsanguis (= *C.* exsanguis) and *Cnemidophorus stictogrammus* (= *C.* burti stictogrammus) are formally named, and a diagnosis and description are given for both. Morphological comparisons between the two are made and variation discussed. Both are characterized ecologically. The type locality for the former is Socorro, Socorro Co., New Mexico. It is a riparian (sub)species that extends upward into the lower part of the Yellow Pine Forest to an elevation between 6000 and 7000 feet.


*Cnemidophorus sexlineatus viridis* is formally named. A diagnosis, description and distribution for the subspecies are given. The type locality is 7.6 mi. south of Tucumcari along St. Rd. 18, Quay County, NM.


Cell band widths are given for *Cnemidophorus inornatus arizonae* (1.2), *C. sexlineatus viridis* (2.5), *C. tigris* (6.7), *C. gularis gularis* (6.9) and *C. burti* (12.5). A positive correlation exists between the number of cells in a lizard and its body size and age. There is seasonal variation in storage and depletion of intracellular "secretory granules". The possession of this structure by Teiids is apparently unique among vertebrates.

Seasonal activity and gonadal cycles are described for *Cnemidophorus inornatus arizonae* from Cochise County, Arizona.


*Cnemidophorus* flagellicaudus and *C. sonorae* are formally named, described and differentiated from *C. exsanguis*. Ecological and geographic distributions are given for all three species, and variation where two or more of them occur sympatrically is discussed.


A karyotypic classification is given for the genus. The partheno-species *Cnemidophorus neomexicanus* is thought to have originated from hybridization between the sexual species *C. inornatus* and *C. tigris*, based on karyotypic evidence. The triploid parthenospecies *C. uniparens* possesses two *inornatus*-like chromosome complements and one attributed to the sexual species *C. gularis*. A hypothesis is presented for the evolution of triploid parthenogenetic species. It is suggested that *C. neomexicanus* is a very recent species, partly because *C. tigris* today occupies successfully and abundantly the most recently evolved major habitat (desert) in the West, and has recently produced within this environment an array of ecotypes and subspecies in all its major subdivisions. The type specimen of *Cnemidophorus perplexus* is thought to be a triploid individual from a cross between *C. neomexicanus* and *C. inornatus*, and specimens referrable to the former indicative of an unsuccessful parthenogenetic event in this genus (see Wright & Lowe, 1967b).


Two hybrid individuals from the Santa Rita Experimental Range in Pima County, Arizona, and their parental species are morphologically and karyotypically described. The hybrids possess 3 genomes from *C. sonorae* and one from *C. tigris*. The hybrid habitat is desert-grassland (mesquite type), elevation 3750 ft. *C. tigris* is by far the most abundant species; *C. sonorae* and *C. uniparens* occur in much fewer numbers and are largely restricted to riparian and open (non-mesquite) grassland habitats. The appearance of desert-grassland habitats during the present century due to environmental changes and the contribution of these changes to hybridization in this genus are discussed. The ecologic trans-
formation discussed has clearly favored desert species. The very real potential for the future evolution of polyploid bisexual species of Cnemidophorus as revealed by the characteristics of the allotetraploids reported here is discussed. It is suggested that males reported previously in parthenogenetic species of this genus are due to hybridization events and not to relictual bisexuality.


31 species are divided into 5 species groups based on chromosome data. The sexlineatus group contains the species burti, exsanguis, flagellicaudus, gularis, inornatus, sexlineatus, sonorae, uniparens and velox; the tigris group contains only tigris, and the tesselatus group contains that species and neomexicanus. The karyotype of the depeal species group appears to be the most primitive among the extant species groups of the genus, and the karyotypes of the other species groups are readily derived from it primarily by means of Robertsonian centric fusions and unequal pericentric inversions. The phylogeny of the genus based on this data is consistent with the overall ecologic and biogeographic distribution of the species. The karyotypically more primitive forms occur in older, more tropical habitats and the karyotypically more derived forms occur in the North American desert.


Cnemidophorus inornatus, C. sexlineatus, C. uniparens and C. velox are treated in the key. The relationship of C. labialis to C. inornatus is discussed.


Cnemidophorus neomexicanus is formally named, and a description and diagnosis are given. The type locality is the McDonald Ranch HQ, 4800 ft., 8.7 miles west and 22.8 miles south of the New Bingham Post Office, Socorro County, New Mexico. Variation and ontogenetic change in the species is discussed, and the distribution as then known is given. Ecological comparisons with other species of Cnemidophorus are made. This species and C. inornatus are common on and around playas. C. tigris is common at the type locality in yucca-grassland bordering
the playa. *C. tesselatus* is marginal in its existence at the type locality, being common to higher zones (and different edaphic conditions) but not those as cool and mesic as favored by *C. exsanguis*. *C. tesselatus* occurs to the apparent complete exclusion of *C. tigris* in an area of yucca-grassland and *Larrea*-"grassland" about 10 miles north of the type locality.


Combined samples of *C. exsanguis* from Bernalillo and Catron Counties, New Mexico, were compared to samples of *C. sonorae* from Cochise County, Arizona. 6 proteins representing at least 9 gene loci were examined; the separate populations of the two forms differ in at least two of them. No intraspecific variation was found.


Protein patterns are given for *Cnemidophorus inornatus*, *C. neomexicanus*, *C. tesselatus*, *C. tigris* and *C. uniparens*. Variations in patterns are discussed. There are interpopulational differences in *C. tigris marmoratus* in New Mexico. The same kinds of differences exist in *C. tesselatus*; sibling species within this taxon are suggested. 25% of bisexual gene loci examined are polymorphic whereas only 10% (6.6% if *C. tesselatus* is omitted) of unisexual gene loci are. *C. neomexicanus* may be a very young species. No variation was found in *C. tesselatus* class E lizards examined. It is suggested that variation in protein patterns of *C. inornatus* and *C. uniparens* supports neutral selection, and that the remainder of the data presented here equivocates between neutral and natural selection (this entire work is poorly done in the opinion of the author of this review).


Several species of *Cnemidophorus* (burti stictogrammus, inornatus, neomexicanus, sexlineatus, tesselatus and tigris) were used. Details of skull morphology, tongue and hyoid musculature, and trunk and limb skeletons are given. New subfamilial arrangements are made. The Teiinae, which includes the genus *Cnemidophorus*, are large in size and actively escape from predators. They are inertial feeders specialized to rapidly ingest relatively small prey.

11 populations in a variety of ecological situations below 6000 feet in the valleys of major river systems were studied for 3 seasons in Colorado. This distribution results from recent dispersal up desert corridors. Pure stands of Sarcobatus vermiculatus and pinyon-juniper woodlands on sandy soils are preferred. Morphology is discussed. The most important food items are Lepidopteran larvae, Coleoptera, Orthopteran nymphs, and spiders. Seasonal shifts in food items are the result of changing acceptibility and availability of prey and a rigid prey size selection standard. Adults and subadults utilize significantly different food sources. Evidence of predation is lacking although 15% of adults have had broken tails. Soil temperatures exert the basic control on daily activity cycles. Seasonal activity lasts from early May until late September. Individual adult males are active for only 60-75 days; females are active for 75-90 days. Lizards spend the inactive season in self-constructed burrows. The reproductive cycle is discussed. Hatchlings average a snout-vent length of 37 mm. Adult size is reached in 13-14 months and reproductive maturity in 22 months. One clutch per year is laid averaging 3.4 eggs (ranging from 2.9-3.9 and increasing with age). Home ranges are not defended and overlap broadly; that of males is larger than that of females. Both size and complexity of home range increase with a lizard's age. A density of 7 lizards/acre was measured for one study area. The sex ratio is 60:40 in favor of males; this is attributed to increased mortality of females during their longer active season. Individual ecological life expectancy is 6 seasons, 4 as a reproductive. The annual replacement in the breeding population is less than 20% (from abstract).


Seasonal changes in the proportions of food items eaten are reported for C. t. septentrionalis in western Colorado. Adult and subadult lizards depend on significantly different parts of the local prey population. The reduction of food competition permits a large annual class of sub-adults to exist, and provides for a more resilient populational response to short-term environmental fluctuations.


3 lizards were found together in a burrow, which is described. This phenomenon is suggested to be a response to extreme winter temp-
The activity seasons for \textit{C. t. septentrionalis} in Colorado and \textit{C. t. marmoratus} in Texas were determined. Older lizards in both areas lay larger clutches. Colorado lizards lay one clutch per year averaging 3.4 eggs; Texas lizards average 2 clutches per year each averaging 2.2 eggs.

Cnemidophorus \textit{laredoensis} from Webb County, Texas, is named, described, and compared morphologically and biochemically. It is diploid and its parental species are most likely \textit{C. gularis} and \textit{C. sexlineatus}.

Distributional notes are given for \textit{Cnemidophorus tesselatus} and \textit{C. perplexus} (= probably velox), as well as morphological descriptions of young and adults of both species. The placement of \textit{Cnemidophorus grahamii} Baird and Girard in the synonymy of \textit{C. tesselatus} (Say) is confirmed. \textit{Cnemidophorus gularis octolineatus} is placed in the synonymy of \textit{C. perplexus}.

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This is the first conclusive report of parthenogenesis in this genus. Museum specimens of *C. exsanguis*, *C. neomexicanus*, *C. tesselatus*, *C. uniparens* and *C. velox* collected at all times of the year were examined, and all were found to be females. A genetic basis for this phenomenon is suggested rather than differential utilization of habitats and/or activity periods by males.


The ecological and genetic hypotheses regarding parthenogenesis are reviewed as they might apply to the genus *Cnemidophorus*. Eggs obtained from wild-caught individuals of 4 presumed parthenogenetic species (*exsanguis*, *perplexus* (= *neomexicanus*), *tesselatus* and *velox*) produced only female progeny. Hatching success was low; this is postulated as a reason for the spotty distribution and/or local extinction of populations of these species, but is also at least partly due to laboratory procedures. The habitat exclusion and inequality of numbers of bisexual and unisexual *Cnemidophorus* where they are geographically sympatric (i.e. *sexlineatus* and *tesselatus* in Colorado) is briefly discussed.

144. —. 1967. Skin grafting in the bisexual Teiid lizard *Cnemidophorus sexlineatus* and in the unisexual *C. tesselatus*. JOURNAL OF EXPERIMENTAL ZOOLOGY 166(1): 137-149.

Pattern classes of *C. tesselatus* from Colorado (A, B, and C) and New Mexico (E) were studied, as well as *C. neomexicanus* from New Mexico and *C. sexlineatus viridis* and *C. tigris septentrionalis* from Colorado. Procedures were tested and rejection criteria were established. Homografts between individuals of isolated populations of *C. tesselatus* are accepted. This species will reject skin grafts from other species of *Cnemidophorus*. Pattern classes A and B from east of the Rocky Mountains are histocompatible. One individual from pattern class C rejects grafts from class A and B individuals but can successfully donate to them as well as to individuals of class E from northern New Mexico west of the Continental Divide. Class E individuals can successfully donate to the other three classes. Northern class E individuals reject grafts from classes A and B but accepts class C grafts. These skin graft reactions are correlated with the triploid nature of pattern classes A and B and the diploid nature of C and E. The lack of uniform results and the small samples used does not preclude the possibility of incompatible clones within the geographic areas of individual pattern classes.

145. —. 1968. Taxonomic problems in parthenogenetic vertebrates.
The systematic treatment of uniparental species is reviewed. They are and have been recognized using all criteria that have been applied to bisexual species (i.e. morphology, ethology, occupying a distinct niche, having geographic range), with genetic isolation of the species gene pool implicit. This logically implies, however, that interbreeding must be able to take place between individuals of that species, therefore the classic species definition is inadequate for parthenoforms. The author favors the Simpsonian evolutionary species concept. Clonal variability within a unisexual "species" is pointed out, and it is suggested that formally naming such makes no more sense than naming genetic strains of laboratory animals or variants in a stable polymorphic species. It is possible that repeated hybridizations between the same two species could give rise to genetically different clones (this, in fact, has almost certainly occurred in Cnemidophorus tesselatus) and that these new gene combinations could be operated on effectively by natural selection without being swamped out, but the author does not favor giving each such clone specific rank. Hybrid parthenoforms will not be genetically adapted to any one habitat or niche and can readily make use of niches, often man-made, that are not occupied, or that are not too firmly occupied. They cannot compete where another species is well entrenched and an integral part of a stable community.


Cnemidophorus neomexicanus, C. tesselatus and C. uniparens were raised through 3 generations in the laboratory. All offspring were produced without benefit of paternal fertilization and all were female.


A general review article, discussing origins, evolution, genetics of parthenogenesis, nomenclatural and systematic problems, and the occurrence of males. 8 male Cnemidophorus tesselatus had been collected from the vicinity of Presidio, Texas, as of June 1968. The chief advantage to parthenogenesis is the ease of colonization of new habitats. Evidence exists that an optimum density threshold must be passed before a parthenogenetic population becomes stable; this implies that single individuals do not found populations. Heavy collecting and commercial alteration of habitat wiped out populations of C. exsanguis and C. tesselatus, respectively. Hybrid parthenospecies are in a sense preadapted because they are not fixed genetically by past selection, although further selection is still possible. Their richer genetic complexion could compensate for their reproductive rigidity. Those that reproduce
through premeiotic endoduplication can acquire and maintain large numbers of chromosomal aberrations and mutations. The importance of synaptic junctions during meiosis no longer exists and each chromosome can evolve independently. New genomes can be acquired through hybridization without disrupting the reproductive process. Access to increased quantities of DNA can be acquired which can be utilized in evolving new mutations without disrupting the balanced array of genes which successfully maintain the species.


Cnemidophorus tesselatus is so efficient in food gathering that just one or two hours of foraging are sufficient for as much as two days. Such efficiency could be an important parameter in a species that must produce several clutches of eggs a season and continue to grow or maintain itself.


A detailed and very interesting investigation into the following questions; a) what specimen constitutes the type, b) where is the type locality, c) with what species in this area may the name be associated? The type specimen is USNM 3060, collected by William Gambel during the last week of July, 1841, in the Rio Grande valley southwest of Santa Fe in Sandoval County. A description of the type is given and it is compared with the species known from the area. It is concluded that the specimen represents that known as C. neomexicanus, which is thus synonymized (NOTE: C. neomexicanus does not now = C. perplexus; see Wright and Lowe, 1967b).


Cnemidophorus gularis, C. inornatus and C. tigris are all essentially confined to the desert plains below 4500 feet; the latter species has apparently been collected in the immediate vicinity only from mesquite dunes bordering the salt flats to the southwest. C. exsanguis and C. tesselatus are common in more open roughland habitats to approximately 6000 ft.

Three study areas near the Rio Grande are described and their vegetation characterized. Rainfall during one study year (1964) was the lowest ever recorded at the NMSU weather station; rainfall during the second study year (1965) was normal. Cnemidophorus exsanguis and C. inornatus preferred mesic habitats of saltgrass-tumbleweed and saltcedar-saltbush during 1964; C. neomexicanus and C. tigris preferred more xeric creosote-mesquite association habitats. All species became more intimately associated throughout the study habitats during 1965. All species except exsanguis expanded into habitats not occupied in 1964 and all species except tigris increased population density. Graphic representations of food items for all 4 species are presented. Lepidopterans were the most important food item for all 4 species. Interspecific competition is reduced by differential prey-size preferences and habitat preferences; neomexicanus and tigris are probably in some competition because of similarities in both parameters. Changes in food items consumed occurred from 1964 to 1965; consumption of lepidopterans increased, that of ants decreased and that of termites ceased. C. exsanguis laid only one clutch of eggs per year, the others laid two. C. exsanguis laid the most eggs and was the most numerous of the 4 species. More males of the sexual species were present in the population during July than females. Seasonal activity is described, with immatures of all 4 species appearing first in the spring, adults appearing by late May and disappearing by late August, and hatchlings remaining active through September. No interspecific differences in preferred temperatures were found. Seasonal daily activity is described; lizards emerged when soil temperatures were 26-30°C. and disappeared when the soil temperature reached 50°C. It is suggested that competition between neomexicanus and tigris is the likely reason the former is distributionally limited primarily to the Rio Grande valley.


Basic techniques used in studying lizard population demographics, including assessing population sizes and reproductive cycles, are presented and discussed. The unreliability of density estimates currently based on walking transects is discussed. Cnemidophorus tigris is one species illustrated.

153. Milstead, W. W. 1953. Ecological distribution of the lizards of
The La Mota Mountain region of Trans-Pecos Texas. TEXAS JOURNAL OF SCIENCE 5(4): 403-415.

The geomorphology, topography, vegetation and climate of the area are described in detail. 8 vegetational-topographical associations are described, and the lizard species found in each are listed. Cnemidophorus inornatus is found only in the ocotillo-catclaw association of mesa tops. C. tesselatus is the most widespread species, occurring in 7 associations. The confusion over the type-locality of this species is detailed, and is herein restricted to "Pueblo, Pueblo County, Colorado: collected on the morning of 19 July 1820 near the mouth of Castle Rock Creek (probably = Fountain Creek)." C. tigris marmoratus was collected from 4 association. It was more numerous than C. tesselatus in two of them and less numerous in the other two; about equal numbers of the two species were collected in the 4 associations. Biogeographical relationships are discussed.


Detailed observations on the ecological attributes of Cnemidophorus perplexus (= inornatus), C. sacki (probably = gularis), C. tesselatus and C. tigris marmoratus were made in Brewster and Presidio Counties, Texas. Foraging activities and behavioral differences are described. Behavioral thermoregulation and microhabitat selection are discussed in relation to seasonal ambient soil temperatures. Data on home ranges are presented for C. t. marmoratus. One lizard recaptured 17 times had a home range calculated as .53 acres, but this study only encompassed 14 days, so this value may be imprecise. Lizards were not territorial. Reproductive data is interpreted as indicating a single long breeding season; however, the data also suggests that two clutches per female are laid. The separation of adult and juvenile activity patterns late in the year is discussed.


Several species (exsanguis, gularis, inornatus, tesselatus and tigris) were studied at 3 locations in Trans-Pecos Texas. Field time of the investigator was limited. There appears to be distinct ecological separation between all the species, with very little overlap. One species always predominates when two occur together in the same vegetation association, while the other is reduced in numbers. The least amount of ecological separation appears to be between tigris and tesselatus; they are the only two species that occur together in the same association. Populations of all the species are disjunct through-
out the area; interspecific competition is implicated. Plains habitats are preferred by gularis, inornatus and tigris whereas roughland habitats are preferred by exsanguis and tesselatus. Competition between a species in its preferred habitat and one "invading" it (i.e. not in the invader's preferred habitat) almost always occurred between a sexual and a parthenogenetic species. Intraspecific aggression occurred, particularly in inornatus, but not on a predictable basis. Interspecific aggression did not occur, although lizards did meet and notice one another. Territoriality was not evident. It was found that a meeting between two lizards is not a common occurrence even where lizards are numerous. Species and geographic differences existed in prey consumption; in general, Isoptera > Orthoptera > Coleoptera > Lepidoptera > Hemiptera. Termites are by far the most important food item and may be regarded as the staple food for all species; indeed, the genus is adapted morphologically for this. Competition for the staple food source is the only obvious explanation for the ecological separation of the species, because size differences and alternate food differences do not allow them to coexist. Differences in foraging activities reflect temperament; inornatus is not easily excited whereas tigris is very nervous and wary, the other species falling between these extremes. Lizards are active only when soil temperatures range between 30-50°C. No interspecific differences in reproduction were observed; multiple clutches are indicated. No competition exists with other lizard genera, they are essentially ecologically invisible. It is possible that individual Cnemidophorus species that are in competitive associations mutually inhibit their own potential increase more than that of the other species and thus can continue to coexist. If, as presumed in this study, no species has an advantage or if reciprocating ones exist, it may be predicted that all 5 species will continue to exist in the Chihuahuan Biotic Province, but weight of numbers or chance will eventually remove all but one of them from any given association within the province.

156. —. 1958. A list of arthropods found in the stomachs of whiptail lizards from four stations. TEXAS J. SCIENCE 10(4): 443-446.

A list as precise taxonomically as possible of the food items eaten by 1141 lizards (exsanguis, gularis, inornatus, tesselatus and tigris) is presented. Taxa are indexed relative to lizard predator and specific locality. No millipedes or lubber grasshoppers (Taeniopoda eques) and only 1 meloid beetle were eaten, indicating unpalatability.


The method of trapping and weather conditions in the mesquite-huisache association are described. Cnemidophorus inornatus, C. tigris and four other species were trapped. No inornatus were recaptured. 38
tigris were marked and 23 recaptured a total of 84 times. One individual recaptured 17 times had a home range of .53 acres based on the outer polygon method. It was noted that tigris makes a low clicking sound when handled.


Cnemidophorus gularis and C. inornatus, which occur in the cedar-savannah association on mesa tops, were virtually wiped out by a 10-year drought while C. tesselatus went from virtually absent to quite abundant.


Drift-fence trapping was done for 5 weeks beginning in June 1 mi. E. of Alpine, Brewster County. The vegetation of the quadrat, located in the short-grass--mesquite association at 4600 feet, is described. Weather during the study period is described. 47 female and 32 male Cnemidophorus sacki (= exsanguis + gularis) were marked and released. 51 lizards were recaptured at least once for a total of 156 recaptures. The average home range was .34 (.25-.43) acres; lizards were apparently not territorial. A modified Lincoln Index gave a density estimate of 20-25 resident lizards per acre. One lizard was eaten by the snake Hypsiglena torquata. Foraging behavior is described; lizards were observed to feed upon scorpions, grasshoppers, termites, candleflies, lepidopteran larvae, and ant lions. Lizards emit an audible squeak when picked up.


Four species of Cnemidophorus in Trans-Pecos Texas (inornatus, sacki (= exsanguis + gularis), tesselatus and tigris) appear to present an example of competition in the absence of an advantage. They occur sympatrically within this region, although all 4 species are seldom found at any one locality, and rarely do more than 2 species occur in equal concentrations. Furthermore, no two species appear to occupy the same ecological associations in the same areas, although all 4 species do appear to occupy the same ecological niche. The diets of all 4 species are similar and have the same staple food items. There is some active intraspecific but no active interspecific competition. Foraging abilities appear to be equal or complementary, and activity periods and
reproductive potentials appear to be the same. The geographic and ecological distributions of whiptails in southwest Texas imply that, although all 4 species are capable of living in most of the ecological associations of the Chihuahuan Desert, no two of the species can simultaneously do so successfully.


Population studies of C. inornatus, C. septemvittatus, and C. tigris done at the Black Gap Wildlife Management Area in 1952 were repeated in 1962. The area had recovered from a severe drought during that time span. Cnemidophorus tigris increased in density in the ecological association it dominated in 1952 as well as in the associations dominated by the other two species. Population estimates were 17.83 /acre and 74.3/acre for 1952 and 1962, respectively. The two other species were quite rare in 1962. Changes in diet are documented; lepidopteran larvae had increased and termites decreased in importance. The evidence suggests a tigris "bloom" and superior short-term competing ability over the other two species based on sheer numbers. C. inornatus and C. septemvittatus are relegated to more xeric, less productive habitats.


The Black Gap area was revisited in 1971 and 1972. The increased rainfall trend has continued. The population density of Cnemidophorus tigris has fallen from 1962 to 13.64 lizards per acre, and C. inornatus and C. septemvittatus have returned to their old habitats. An increase in groundcover and predation are two hypotheses advanced for the population phenomenon in C. tigris. Natural cyclic events and the ability of C. tigris to "bloom"—take best advantage of short-term favorable events better than other species of Cnemidophorus—are also discussed. Changes in diet over the two decades are discussed. It is concluded that termites are the staple food for Cnemidophorus during lean months and/or years, but not during periods of abundant food variability and availability.

Eleven habitat associations are described for the plateau, which is considered to lie in the northeastern portion of the Chihuahuan Biotic province. *Cnemidophorus grahamil (= tesselatus)* was taken mostly in cedar-octillo at the base of mesa slopes or in mesquite-creosote not far from its margin with the former association. Both are characterized by extensive rock and sparse vegetation. *Cnemidophorus gularis* and *C. perplexus (= inornatus)* were found in cedar savannah of mesa tops and mesquite-creosote of the broad inter-mesa valleys. The former species was more common than the latter. The habitats occupied by these two species were characterized by good vegetative cover, almost impenetrable in places, and little rock.


An analysis of food items eaten by *Cnemidophorus tigris marmoratus* is given. It is an opportunistic feeder on arthropods, predominately coleopterans and orthopterans. Competition with the other dominant lizard species present, *Uta stansburiana*, is avoided through the exploitation of different size-classes of prey. Interspecific competition for food is one explanation for the rarity of other lizard species in the study areas.


*Cnemidophorus tigris marmoratus* is very plentiful on desert flats and sandy areas along the Rio Grande. It is less abundant in foothills and rare or absent in prairie areas or elevations above 5000 feet. Intrasp...
The densities of 4 species of Cnemidophorus (inornatus arizonae, sonorae, tigris gracilis, and uniparens) were estimated by walking a line transect. Four study areas manifesting complex habitats are described. All species did not occur on all areas. C. inornatus densities ranged from 2.5/hectare at the end of May to 15/hectare at mid-July on the same site. C. tigris and C. uniparens ranged from 2-11 and 4.5-18 lizards per hectare, respectively, at the same times on different study areas. Only 8 C. sonorae were seen during the entire study. Daily and seasonal activity patterns and food items were determined. Measurements of niche breadth and niche overlap were compared for syntopic species pairs and ecological differences between bisexual and unisexual species were found to be minimal. The most important niche components separating the species studied were macrohabitat, microhabitat, time, and food, although there is high overlap in the latter three. It is concluded that these 4 species form a guild of similar lizards.


An individual of C. i. arizonae possessed male organs on the left side and female organs on the right side of its body internally. A photograph is presented.


The Chihuahuan Desert is defined by climatological, physiographical and vegetational criteria. It may be defined as the North American warm desert east of the Continental Divide. It possesses great internal homogeneity. Cnemidophorus inornatus, C. neomexicanus and C. tesselatus are considered to be characteristic or endemic.


A monumental effort. The paleoclimatology and geologic history of the Chihuahuan Desert are examined as reflected by the herpetofauna. The region encompasses 450,000 km² from latitude 22N to 35N and longitude 101W to 108W. Nine species of Cnemidophorus (burti, exsanguis, flagellicaudus, gularis, inornatus, neomexicanus, tesselatus, tigris,
and uniparens) are considered here. Five of them are parthenogenetic, and all 5 are endemic to the Trans-Pecos (northernmost) subprovince of the Chihuahuan Desert. C. neomexicanus has the lowest ecologic amplitude of the 9, restricted to Chihuahuan desertscrub and desert riparian associations between approximately 600 and 750 m. elevation. C. exsanguis has the widest, occurring continuously from scrub associations at approximately 550 m. to montane coniferous forest at 2000 m. There is considerable overlap between the species at this ecologic scale with no fewer than two occurring together in any association at any elevation (and this minimum case occurs only at each extreme of the elevational continuum for the genus). The Wisconsin glaciation virtually eliminated the Trans-Pecos subprovince as a desert. The post-Wisconsin Xerothermic Period (12000-5000 years B.P.) represents an extreme in Quaternary warm arid conditions and is the most recent in an alternating series between warm-dry and cool-moist Pleistocene climatic episodes. Desert biota re-invasions of the Trans-Pecos subprovince must have taken place over huge areas in relatively short periods of time, perhaps expanding 3-5 km/year, resulting in broad ecotonal herpetofaunas often with species densities exacerbated by an edge effect. It is precisely this complex overlapping of fluctuating ecological associations (such as between desert, grassland, and pinyon-juniper woodland) that may have played a critical role in the origin of hybrid parthenogenetic Cnemidophorus. They are at present maintained in ecotonal conditions resulting from these shifts. They are absent from the other subprovinces of the Chihuahuan Desert due to historical factors and/or longer climatic stability in those regions.


The habitats at two collecting localities, Dark Canyon and Frijole, are described. Cnemidophorus sexlineatus sackii (= exsanguis) was the most frequently seen if not the most common reptile in the Guadalupe Mountains. It was very abundant at the bottom of Dark Canyon but much less common on its rocky slopes.


Cnemidophorus tigris from the Mojave and Colorado deserts were used in the experiments. Lizards were kept under (a) food only and (b) no food or water conditions; tigris survived well under (a) supporting the general assumption that desert lizards balance water loss with pre-formed water in the diet. Water loss at 30°C in still, relatively dry air (36% R.H.) was 0.58 mg/gr/hr. The vital exsiccation limit was 44.91 (loss in % initial body weight). C. tigris survived an average of 30 days under condition (b); one less xerically-adapted species sur-
vived only half as long whereas 3 more xerically-adapted species survived considerably longer. Interspecific water loss rates have not yet been determined in the Teiidae as yet, but the emerging pattern for reptiles is a close correlation between loss rate and degree of habitat aridity.


Electrophoresis was performed for several enzymes on various species of Cnemidophorus. Lizards from Colorado, New Mexico and Texas were used in the analyses. Adenosine deaminase (ADA) is polyallelic and controlled by a single autosomal locus. ADA phenotypes are: C. septemvittatus (ADA-1), C. gularis (ADA-2), C. sexlineatus and C. tigris (ADA-3), C. inornatus (ADA-4). Parthenogenetic species examined have the following ADA phenotypes: diploid C. tesselatus 1-3, triploid C. tesselatus 1-3-3, C. neomexicanus 3-4, C. uniparens and C. velox, 3-4-4, and C. exsanguis 2-3-4. Parthenogenetic phenotypes were compared with mixtures of suspected sexual parental phenotypes and were found to be virtually indistinguishable. Thus, diploid C. tesselatus are the result of (a) hybridization event(s) between C. tigris and C. septemvittatus. Evidence from karyotypes and lactate dehydrogenase (LDH) genotypes indicate that C. tigris and not C. sexlineatus was involved in the above event(s). The evidence likewise indicates that triploid C. tesselatus arose from cross(es) between diploid tesselatus and C. sexlineatus. C. sexlineatus is also homozygous for an allele of 6-phosphogluconic acid dehydrogenase (PGD) not found in the other sexual species; triploid tesselatus possess this allele in a single dose with a double dose of the other allele. The evidence also indicates that C. tigris X C. inornatus event(s) led to C. neomexicanus. The origins of the remaining 3 parthenospecies in unclear, and does not appear on the basis of available evidence to involve any possible combination of the 5 sexual species studied here. For each enzyme surveyed among the parthenospecies, only a single characteristic heterozygous genotype was observed in all individuals of each species. This, plus evidence from histocompatibility work, suggests that all diploid tesselatus may be genetically identical and hence derived from one unique interspecific hybridization.


A hybrid C. exsanguis X C. inornatus collected from a weed bed between railroad tracks and the city zoo in Alamogordo, New Mexico, possesses a tetraploid chromosome complement. The hybrid habitat supports dense populations (50 and 10 lizards per acre, respectively) of the two parental species. A detailed description of the aberrant li-
zard is given, including behavior in captivity where it laid 2 eggs. Captive courtship and mating behavior between C. inornatus males and C. exsanguis and C. tesselatus females is described in detail. This type of behavior is probably due to (or at least facilitated by) crowding in captivity, but since the population from which the natural hybrid came from was dense, perhaps overcrowding (high density) is required for interspecific hybridizations to occur. The cytological events leading to tetraploidy in Cnemidophorus are discussed, and a very interesting summary of genetic mechanisms of parthenogenesis and the implications thereof is given. It is suggested here that triploid C. tesselatus arose from a single hybridization event between diploid tesselatus and C. sexlineatus. The absence of tetraploid species of Cnemidophorus is attributed to the rarity of achieving parthenogenetic competence in interspecific hybrids. Interspecific hybrids are not rare (witness the C. perplexus situation plus events like the aberrant individual reported on here) so the achievement of parthenogenetic competence is the critical event.


Lactate dehydrogenase (LDH) isozymes consist of two distinct subunits, A & B, associated in tetramers; there are thus 5 possible subunit combinations. Subunit synthesis is controlled by structural genes at two distinct loci, a & b. The sexual species Cnemidophorus tigris, C. inornatus and C. gularis, and the parthenogenetic species C. exsanguis all possess the same A subunit, but C. tigris possesses a B variant, B'. Electrophoresis of C. neomexicanus and C. tesselatus E reveal more than 5 possible LDH subunit combinations (= heterozygosity), thus 3 different subunits (A, B, and B') must be present. C. tigris is therefore implicated as one parent for both of the preceding hybrid parthenogenetic species. Electrophoretic patterns reported on here are very similar to those of other vertebrate hybrids, both natural and artificial.


The densities of electrophoretic bands of heterozygous triploid Cnemidophorus tesselatus are unequal, showing higher proportions of B over B' subunits of LDH. These proportions are consistent with the explanation that each allele is expressed equally, therefore the diploid tesselatus genotype is b'/b and the triploid genotype b'/b/b. The b' allele is contributed by C. tigris and the b allele by one or more species of the sexlineatus group of Cnemidophorus.

*C. exsanguis* (= probably *flagellicaudus*) occurs between 4000 and 5000 feet, most commonly along drainage channels with *Quercus* or open areas with *Juniperus*. *C. tigris gracilis* is very abundant below 4600 feet, but most common between 3200 and 4400 feet in elevation. It occupies relatively open Prosopis-Acacia-Opuntia desert, moving at the periphery of shrubs. *C. uniparens* occurs from 3200 to 5000 feet in riparian habitats along streams and washes.


Female parthenogenesis has repeatedly evolved in most major animal and plant groups. Although the taxonomic distribution of parthenogenetic "morphospecies" suggests that they are unsuccessful over evolutionary time, parthenogenesis ranks as one of the major exceptions to the Mendelian cycle of meiosis and fertilization. Data summarized indicate that most, if not all, secondarily-evolved parthenogenetic morphospecies are clonally diverse. The nature of interactions among sympatric clones of such species are presently ambiguous. Factors influencing the dynamics of clonal diversity include (1) the mode of clonal origin (2) the pattern of environmental heterogeneity (3) vagility and (4) interactions with sexual ancestors. The outcome of competition between a parthenogenetic taxon and its sexual ancestors is unclear. Models can be generated which give any outcome depending on initial assumptions and the role of clonal diversity in the parthenogen has received little attention. The polyphyletic diploid morphospecies *C. tessellatus* is characterized by low clonal diversity and the presence of one dominant clone. Much stronger selection is envisioned among polyphyletic clones because of their greater genetic differences than among monophyletic clones. This distinction will become blurred with time, but this has not occurred yet as the affinities of clones to each other and their ancestral species can still be determined by electrophoresis. Unpublished data is reported which shows that *C. neomexicanus* has low clonal diversity with only 2 clones detected over the entire species range and with no multiclonal populations.


Morphological consequences of parthenogenesis in *C. tessellatus* were studied as reflected in the concordance of morphological variation with electrophoretically-detected clonal heterozygosity.
The relative amounts of phenotypic variation in populations differing in clonal structure were compared with populations of one parent species, *C. tigris*. *C. tesselatus* consists of at least 18 diploid and 3 triploid clones. The presence at some loci of different heterozygous genotypes involving different electrophoretic morphs found in the parental sexual species suggests multiple hybridizations as a major factor in generating clonal diversity. The presence of unique alleles in some clones and histocompatibility between pattern classes indicate that some clones may have diverged from a common ancestral clone. 14 morphometric characters of the two species were subjected to univariate and multivariate analyses. Six of 23 tesselatus populations sampled are multiclonal. Seven clones were discovered at Conchas, San Miguel County, New Mexico; heterozygosity at one locus is probably due to multiple hybridizations. The population at Higbee, Otero County, Colorado consists of both diploid and triploid individuals. Diversity in the remaining 4 multiclonal populations was low with no detectable morphological variation among clones. Variability in size- or growth-related characters adjusted for allometry and covariation with size is similar in both species. Variation in 6 of 9 scale characters differs consistently as expected between sexual and parthenogenetic populations.

How the sympatric clones of the *tesselatus* complex coexist is unknown. Specimens from the two most clonally diverse populations reported here were collected on weedy roadsides and around trash piles and abandoned houses; perhaps clonal diversity is the result of nondirectional environmental perturbations which have not permitted any one clone to competitively replace the others. However, the morphological discontinuities among clones may very well reflect differences in niche utilization or physiological attributes. It is suggested that environmentally-induced variability obscures genetic variability of size characteristics measured in the two species. It is also suggested that the genotypes of parthenogenetic and sexual taxa differ in their phenotypic responses to environmental change. Genetic variability for phenotypic plasticity in a sexual ancestor will be "fixed in" to different degrees in different clones; eventually in temporally or spatially changing environments surviving clones may be highly flexible general-purpose genotypes. Interactions among genes may be qualitatively different in parthenogenetic and sexual genomes. Epistasis and dominance between the parental genomes of diploid *tesselatus* are more important than additive effects in determining mean character values in this study, whereas in sexual species genes are selected primarily for their additive effects. The mutational load carried by clonal lineages is greater than in individuals of sexual species, although this does not seem to be the case in *Cnemidophorus tesselatus*. Naturally occurring parthenogenetic organisms would appear to be useful models for examining relationships among genotype, phenotype, and ecology of populations.

The understanding of the evolution of sexual reproduction hinges on how organisms resolve the conflict between immediate genetic fitness and maintenance of genetic flexibility. Parthenogenetic individuals maximize their genetic representation in future generations and maintain any adaptive gene combinations. Sexual individuals produce genetically diverse offspring (and populations) which may be less prone to extinction in uncertain environments. Comparative genetic, morphological, and ecological studies of related parthenogenetic and sexual populations are critical.

Multivariate analyses were done on 13 morphological traits of diploid and triploid population samples of Cnemidophorus tesselatus and females of the parental species C. septemvittatus, C. tigris and C. sexlineatus. Comparisons were made only from broad areas of sympatry. Characters for diploid tesselatus were summarized in a weighted hybrid index which maximized the separation between the two parental species. Diploid tesselatus were phenotypically closer to septemvittatus when all 13 characters were compared. They were closer to tigris when the 9 scale characters were considered alone, and intermediate between the two parental species when the 4 size-correlated characters were considered alone. The first two character groups also differentiate the two parental species well from each other whereas the latter group does not. Triploid tesselatus are phenotypically closer to diploid tesselatus than to sexlineatus in all cases. However, the estimated probability that any given unknown sample of triploid tesselatus will actually belong to one of the parental groups is less than .001. No diploid population has a probability greater than .01 of belonging to either parental species when all 13 characters are considered. All diploid populations have a probability greater than .05 of belonging to either of the parental species when size characters are considered alone; when considering the 9 scale characters alone, 17 of 51 diploid samples have a probability greater than .05 of belonging to C. tigris.

Most characters in diploid tesselatus show dominance or overdominance in averages and wide ranges of expression among clones and populations, indicating differing epistatic or genotype-environment interactions between the various parental genomes responsible for the origin of diploid tesselatus. Two and four unique clones occur in the vicinity of Engle (Sierra Co.) and Conchas Lake (San Miguel Co.), New Mexico, respectively, indicating multiple hybridizations between septemvittatus and tigris. It is suggested, based on this, current distribution and possible distributional history, major habitat preferences, and similarities in size, that C. tesselatus and female C. septemvittatus compete with each other and are in ecological, if not evolutionary, equilibrium. The implication is that tesselatus is competitively superior under certain conditions. It is suggested that this can be tested with experimental field studies comparing reproduction in sympathy and allopatry. Multiple hybridizations are the most important source of morphological heterogeneity in C. tesselatus which represents a complex of clonal microspecies. The effects of this heterogeneity among clones on their fitness are unknown; it is likely that discontinuities reflect differences in adaptation, allowing local or regional coexistence of clones.

An analysis of allozymic variation in proteins encoded by 21 loci of diploid and triploid populations of C. tesselatus sampled throughout its range, as well as selected samples of the parental species (sexlineatus and tigris marmoratus in New Mexico), is reported. All triploid tesselatus represent a single clone, but 12 different diploid clones were identified with 1 to 4 clones recorded in each population sampled. Three possible sources of clonal diversity are discussed. It is suggested that C. tesselatus is of relatively recent origin and that the evolutionary potential of it and other parthenoforms is not as limited as heretofore considered.


Seasonal activity, growth rates, tail-break frequency, population structure and density, and reproduction are discussed. Comparisons are made with earlier studies on this and other species. The mean distance between captures was 16.2 m for 29 immatures and 21.9 m for 53 adults. Tail-break frequency was relatively low in juveniles (5-10%) and high in adults (30-56%). Growth rates ranged from 1.3 mm/month in adults to 5.0 mm/month in juveniles. Some juveniles reached minimum adult size in less than one year, but others did not do so until almost 2 years old. Females were gravid from April to early August and laid at least 2 clutches averaging 2.05 eggs each. Males had enlarged testes from March through July. About 70-80% of the population was potentially reproductive during the breeding season. Hatchlings emerged from mid-June or early July through September. C. tigris gracilis appeared equally abundant on 2 flatland desert and 3 low altitude (450-500 m) montane study areas. Density in a third flatland area was about 13/ hectare in spring and 36/hectare in late summer. Lack of male territoriality is inferred from the presence of 5 male and 2 female lizards in the same pitfall trap on one occasion. No aggressive behavior was observed in over 400 hours of field work.


Cnemidophorus exsanguis and C. tesselatus from southern New Mexico lay 2 clutches per year. Gravid females of the former were collected from May 24 to July 12. Females collected on 14 and 29 June were beginning their second clutch. Gravid females of the latter species
averaged 92 mm SVL (range 82-101). Clutch size was 3.9+ .53 (1-6). Egg weight was 11-12% of body weight. Immatures ranged from 56-79 mm SVL. Adult females were collected from 10 May to 10 August. Oviducal eggs were found from 24 May until 12 July. C. tigris seasonal and sexual activity is shorter in Utah than in Arizona and New Mexico. The length of male sexual activity in Arizona > New Mexico-Texas > Utah. The average size of mature males in Utah > New Mexico-Texas > Arizona. Females possess oviducal eggs for 1 month in Utah, 2 months in New Mexico and Texas, and 3 months in Arizona. The frequency of gravid females collected peaked in June-July in Utah, declined steadily between May and July in New Mexico and Texas, and peaked in April and June in Arizona. Utah females averaged twice as many eggs per clutch than the others; the pattern of female size at maturity followed that of males. Hatchlings were first seen 4 September in Utah, 1 August in New Mexico, and 14 June and 7 July in two different years in Arizona. Fat body cycles are described.


The somatic cells of Cnemidophorus neomexicanus, C. tigris septentrionalis, C. velox, C. tesselatus and C. exsanguis possessed 46, 46, 68, 69, and 70 chromosomes, respectively; therefore, the latter three are triploid. The generalized karyotype is described. The triploids appear to consist of 3 separate sets of chromosomes rather than a complement resulting from fragmentation of the basic set found in bisexual species.


Several species (gularis, inornatus and 3 subspecies of tigris (probably gracilis, marmoratus and septentrionalis)) possess a 2N chromosome number of 46. The first two species' karyotypes are nearly identical in appearance and have a fundamental number of 48. The latter species' fundamental number is 52. C. perplexus (= neomexicanus), C. velox, C. tesselatus, C. uniparens and C. exsanguis possess chromosome complements of 46, 68, 69, 69, and 69-70, respectively; the first species is diploid and the remainder triploid. C. inornatus and C. tigris are implicated as the parental species of C. perplexus. The remainder of the parthenogenetic species can be derived, although not unequivocally, karyotypically from various combinations of inornatus and tigris. Karyotypic variation is found in different populations of exsanguis. The author is opposed to formal taxonomic revisions within these parthenogenetic species until variation within them is better understood (from abstract).

Ten flatland desert sites were studied from southern Idaho to southern Arizona. The number of lizard species present in each area was correlated with horizontal and vertical components of spatial heterogeneity (vegetation and possibly substrate). Each area had from 4 to 10 species, increasing from north to south, out of a possible total of 12. Convexity is defined as the sum total of variables regarding food preferences, substrate characteristics, and foraging behavior. \textit{Cnemidophorus tigris} is the only teiid represented; it exploits the environment by constantly moving from cover to cover, pausing occasionally to dig or climb for prey. It is the only widely foraging diurnal species in this system, and is thus the most "convex".


This study encompassed the Great Basin, Mojave and Sonoran deserts; \textit{Cnemidophorus tigris} was the only teiid present. Eight mechanisms for the determination of species diversity using lizards are examined. It is concluded that ecological time, spatial heterogeneity, length of growing season, and amount of warm season productivity are all pertinent factors, but that the most important single factor is spatial heterogeneity (mainly vegetative) of the environment. It is suggested that climatic variability allows the coexistence of many different plant life forms, the variety of which in turn controls the number of lizard species present. This study spotlights the lack of same in New Mexico where lizards, particularly the genus \textit{Cnemidophorus}, are very diverse in desert environments (opinion of this reviewer).


The subspecies \textit{tigris}, \textit{gracilis} and \textit{aethiops} were studied from southern Idaho through northern Sonora. Lizards in the north emerge in May and aestivate during midsummer months; those in the south are active from April through late August. Daily activity periods are similar for all populations studied, although time of emergence tends to be later in the north. Daily patterns are bimodal with much more activity in the morning than the afternoon. There is a significant positive correlation between estimated lizard abundances and total precipitation during the previous 5 years, suggesting that abundance is correlated with food supply. There is a latitudinal cline exhibited in mean body temperature of active lizards; lizards of northern populations are ac-
tive at lower air and body temperatures. Termites are the major food for southern populations, beetles and grasshoppers for northern populations. Seasonal food trends are evident; insect larvae are an important early food source for all populations. Lizards eat a wide variety of food types where primary productivity is low and specialize more where it is high. Greater food competition with other lizard species in the south as well as the lack of termites in the Great Basin desert may account for some of these differences, in the opinion of the author of this review. Foraging behavior is described. Southern populations are subject to greater predation. Fat body size is not correlated with latitude but is inversely correlated with long-term average annual precipitation. It is suggested that lizards from less productive areas must allow themselves a greater margin of safety due to more probable occurrence of drought. Northern lizards breed only once a year but lay significantly larger clutches than southern lizards, which lay at least 2 clutches annually. Clutch size appears to be flexible in response to resource availability. There is a significant correlation between mean clutch size and deviation of the short-term (last 5 years) mean precipitation from long-term mean precipitation. Ecological challenges for northern lizards are primarily physical and largely climatic, whereas biotic interactions assume relatively greater importance for southern lizards.


The latest on the technique is reported, with Cnemidophorus tigris from Nevada one of 5 species used.

189. —. 1981b. Use of scutellation for distinguishing sexes in bisexual species of Cnemidophorus. HERPETOLOGICA 37(4): 244-249.

Males of several species of Cnemidophorus (including gularis, inornatus, sexlineatus and tigris from New Mexico) possess a row of slightly to distinctly enlarged scales on either side of the ventral surface of the tail, distally separated from the vent by 2-4 granular scales, called the postanal ridge. Immediately posterior to each ridge is a distinctly shaped enlarged scale, the postanal plate. Females possess the former but not the latter. The utility for use of this character in field studies in view of the lack of other reliable sex determining mechanisms is discussed, along with variation of the trait. Small series of several parthenogenetic species demonstrate only the female characteristic.

190. Presch, W. 1974a. Evolutionary relationships and biogeography of the macrotelid lizards (Family Teiidae, Subfamily Teiinae). BULL-
An analysis of 25 osteological character states is presented for 9 genera; species of *Cnemidophorus* used include *burti*, *exsanguis*, *gularis*, *inornatus*, *neomexicanus*, *sexlineatus*, *sonorae*, *tigris*, *uniparens* and *velox*. The genus was extant during the Oligocene and evolved in isolation from other genera of the family in North America through much of the Cenozoic.


The dental morphology and tooth types are described for 9 genera, including all the species of *Cnemidophorus* mentioned in the previous paper. The genus can be divided into two groups based on the criteria.


Data are presented for the first time for *Cnemidophorus exsanguis*.


*Cnemidophorus cf. sexlineatus* is present, and comments on paleoclimatology are made.


*Cnemidophorus* spp. are included in the fauna. Species composition indicates altitudinal fluctuation of vegetation zones in the Guadalupe Mountains due to climatic changes during the late Wisconsin.

The collection was made during July and August in the vicinity of Alamogordo, New Mexico, and Tucson, Arizona, respectively. The habitats, geology and climate of the areas is described, as well as specific collecting sites. *Cnemidophorus gularis* (= *exsanguis*) is common at Alamogordo in the lower part of canyons and in stony arroyos on alluvial slopes. It (= *flagellicaudus* and/or *sonorae*) occurs in the same habitats at Tucson, as well as along the Santa Cruz river in willow-poplar associations. Other habitat and morphological details are given. Beetles and ants make up the bulk of the stomach contents. *Cnemidophorus melanostethus* (= *tigris* + possibly *tesselatus*) is very common in the creosotebush association of alluvial slopes near Alamogordo and is exclusive to it there. It (= *tigris*) occurs in greasewood plains and creosotebush of mesa arroyos near Tucson. Behavior and morphology are discussed. *C. sexlineatus* (= *inornatus*) occurs in the mesquite and Atriplex associations and on the White Sands near Alamogordo. Ants, grasshoppers and spiders are eaten. Morphology is described.


The specimen was collected 1 mile east of Presidio, Texas, in the Rio Grande valley. *Cnemidophorus tigris* was sympatric. Sexual behavior between the male and a female *tesselatus* is described. Motile sperm were produced by the male but none were present in the female and she never became gravid.


The Presidio Basin is limited to the floodplain of the Rio Grande. Its soils, vegetation and agriculture are characterized. Black and white photographs of the study areas and of *C. tesselatus* (juvenile-subadult-adult) are provided. *Cnemidophorus tesselatus* is mostly confined to the Basin in this area. It occurs in isolated populations but not only in rocky areas—it is also found in backyards and abandoned lots in the town of Presidio, and on levee and farm roads. It is associated with disturbed areas where it is found on surrounding desert mesas. Daily activity is confined between 9 a.m. and 3 p.m.; soil and air temperatures at the beginning of activity are 32 and 30°C, respectively. Cloacal temperatures of active lizards average 39.5°C. Gravid lizards have apparently restricted activities. Domestic cats are by far the most important predator, with snakes next. The activity season extends from March to November with the bulk occurring from mid-May to mid-August. Soil temperature is the critical factor for activity. Hatchlings appear at the beginning of July and grow to subadult size (50–69 mm) before entering hibernation. Lizards rare-
ly live to their fourth, and never to their fifth, activity season. Yolked follicles are present in April and oviductal eggs in May-June. The minimum reproductive size and age is 70 mm SVL and 13-14 months, respectively. Two clutches per year averaging 3.7 (1-8) eggs each are laid, larger females laying larger clutches. Incubation time is 63 days; other reproductive aspects are discussed. Fat bodies are depleted during the reproductive season and are replenished before hibernation. They are used mainly for the first clutch and not the second. Fat is also stored in the tail. All fat is used mainly for reproduction. 5 senile females (very large fat bodies and minute or non-existent ovaries during the reproductive season) were collected; they are probably 4th-year females. Pesticides are not retained from one activity season to the next. The diet of lizards was analyzed; lepidopteran larvae were the most important food item followed by orthopterans and spiders. Pesticides were acquired through food ingestion. Lizards avoided cotton rows next to roads and levees where the pesticide concentration was very high. They became active in the morning after spraying was completed and thus were not directly exposed. Fat mobilization for the first clutch occurred in May whereas heavy application of pesticides did not occur until June. Fat body replenishment occurs after pesticide application decreases, therefore this species is potentially exposed to minimal hazards from pesticides.


A photograph of a specimen with fully developed testes and reproductive organs collected on alluvial soil of the Rio Grande valley 1 mi. E. of Presidio is provided. The area was formerly cultivated and is now wild. The specimen is morphologically described.


Five species (exsanguis, gularis, inornatus, tesselatus and tigris) were studied in the Big Bend region of Texas. All have different habitat associations, which are briefly discussed. Thermal characteristics vary among each of 3 microhabitats within 5 major habitats studied. Data on 3 different environmental temperatures and body temperatures taken during 3 different types of behavior are given for each species. Differences in thermal characteristics are thought to reflect fundamental behavioral differences between species. Thermoregulatory behavior in the wild and of 2 species (exsanguis and tesselatus) in artificial thermal gradients is discussed. Overall mean body temperatures of actively moving lizards are very similar among the species studied and suggests that optimal body temperature is an evolutionally conservative trait of whiptails. Cnemidophorus has among the highest
body temperature values recorded of any lizard genus. Species variation in thermal characteristics reported is due to recently evolved differences in habitat niches, individual seasonal differences associated with reproductive and nutritional state, and behavioral trade-offs between maintaining the optimal body temperature and maintenance activities such as foraging.


Cnemidophorus exsanguis, C. gularis, C. inornatus, C. tesselatus and C. tigris were studied in southwest Texas. If the unisexual species are animal weeds, they should possess relatively r-selected reproductive traits compared to sympatric bisexual forms. Reproductive effort (RE) was estimated by clutch weight to body weight ratios. RE varies interspecifically, partly as a result of differential habitat preference and productivity. Clutch size and egg weight is partially correlated with female body size. A minimum egg size is suggested; too small and young cannot compete successfully. No differences in RE were observed between the bisexual and unisexual species studied here, except for the higher intrinsic rate of increase for the parthenoforms. Reproductive strategy of a particular species of Cnemidophorus is probably related to its ecological position. Any differential selective factors operating on static reproductive characteristics may be overshadowed by constraints imposed by body form, size, and foraging techniques.


This paper examines the hypothesis that escape tactic diversities should vary positively with predation pressure among conspecific prey populations and escape tactics should diverge among similar sympatric species that share predators. Escape behavior was quantified for Cnemidophorus tigris at many sites where it occurs alone and for an assemblage of Cnemidophorus species (exsanguis, gularis, inornatus, tesselatus and tigris) in southwest Texas. Predation pressure was estimated by tail-break frequencies. Escape behaviors are described for species. Sympatric whiptail species differ significantly in escape behavior; escape behaviors are more divergent than if each species evolved escape tactics independently of other species in a random fashion. Cnemidophorus tigris exhibits a reduced tail-break frequency in southwest Texas than at more westerly sites where it occurs alone but with presumed similar predation pressures, perhaps as a result of increased protection offered by a species assemblage with diverse escape behaviors.
Habitat differences are sharply defined between *Cnemidophorus grahamii* (= *tesselatus*), which lives in canyons, and *C. tessellatus* (= *tigris*), which occupies desert flats or plateaus.

Histological studies were done on specimens from Tom Green County, Texas. Males emerge from hibernation with relatively small testes which rapidly increase in size to a maximum in May followed by gradual gonadal regression until September. This parallels female ovarian cycles. Fat bodies are almost depleted during the cycle.

Field studies of sympatric relationships among *Cnemidophorus exsanguis*, *C. gularis gularis*, *C. inornatus heptagrammus*, *C. tessellatus E* and *C. tigris marmoratus* were conducted to obtain a better understanding of speciation processes in the genus. Populations of all the species in the region were compared morphologically and 2 new pattern classes of *C. tessellatus* described. Geographic and ecological distributions are discussed in detail. Minor differences in food items between species are thought to be important during adverse times. Species behaviors are discussed; *C. inornatus heptagrammus* was found to be the most aggressive species under captive conditions. Foraging behavior was found to be a significant measure of niche separation. Reproduction was investigated; all species produced 2 clutches a year. Unbalanced sex ratios favoring males found in *C. tigris marmoratus* is thought to be a contributing factor in the hybrid origin of *C. tessellatus*. Ecological and evolutionary sympathy and competition is discussed. Changes in species composition and density due to yearly climatic fluctuations were observed.
most distinguishing features between *C. dixoni* and *C. tesselatus*; the most important differences are ecological. The geographic distribution and habitat of *C. dixoni* in west Texas is discussed in detail, and the sympatric ecological relationships with *C. tesselatus* and its generating species is discussed. Two pattern classes (A & B) of *C. dixoni* are recognized; *C. tesselatus* F from Hidalgo County, New Mexico, is referred to *C. dixoni* B. (The author of the present review has important comments on this paper in the introduction).


There has been an increase in *Cnemidophorus tigris* populations in the Fort Stockton, Texas, area at the expense of *C. gularis* and *C. inornatus* over the last several decades due to increased human-influenced aridity.


Food items eaten and foraging behavior are discussed in detail for *Cnemidophorus exsanguis*, *C. gularis*, *C. inornatus*, *C. tesselatus* E and *C. tigris*. It is concluded that minor differences existing between the species in types and proportions of food items eaten could be important in adverse times. Foraging behavior among sympatric species represents differences in methods of obtaining food, and thus represents niche segregation.


*Cnemidophorus exsanguis* and *C. gularis* were studied in Brewster County, Texas. Individuals of the former species reached reproductive maturity at the age of 10 months, but most females of the latter species did not mature until their second potential reproductive season. Snout-vent lengths and clutch size were directly proportional. Older females of both species produced 2 clutches per year.

The escarpment is described relative to its location, climate and vegetation. Its influence on herpetofaunal distributions is discussed. Cnemidophorus gularis gularis and C. sexlineatus reach their eastern and western range limits in Texas here, respectively.


The correct and currently recognized assignment of the names C. tesselatus (Say) and C. tigris Baird and Girard is made.


A supplementary list of published accounts and records, as well as range maps, are given for several species of Cnemidophorus (sexlineatus, tesselatus, tigris septentrionalis and velox) in Colorado.


P. cnemidophori in Cnemidophorus tigris and P. warneri in C. inornatus represent new host and distributional records, respectively.


The species' habitat in the Mazatzal Mountains of eastern Arizona is briefly described. Average body temperature was 39.9±0.3 degrees C. Clutch size was 4.3±0.4 eggs; only one clutch per year was produced. Egg production began in early May and eggs were deposited in June-July. Lizards began stockpiling body fat in August and entered brumation by September.

The Paloduro region consists of a series of canyons and draws, with scattered cottonwoods and willows in their bottoms. Other vegetation includes scrub oaks, Opuntia, bear grass and various shrubs. Elevations range between 2800 and 3600 feet. Cnemidophorus gularis is abundant in some areas, but not where C. grahamii (= tesselatus) occurs. The former species prefers sandy level areas and the latter rocky bluffs. C. grahamii (= tesselatus) does not attempt to escape into or even use burrows, but seeks shelter under rocks (perhaps because they are abundant). The species was particularly common in Rush Creek Arroyo around large sandstone rocks on bluffs surrounding a series of small springs. One individual was found depositing eggs in loose sand near the base of a shelving bank. Morphological descriptions of adults and young are given.


A list of museum specimens is given and localities individually plotted on range maps. Species of Cnemidophorus included are exsanguis, gularis, inornatus, sexlineatus, tesselatus and tigris.


The abundance of Cnemidophorus tigris on a daily and seasonal basis was determined in a lizard community of 4 species on the Nevada Test Site. Individuals of C. tigris were found to escape capture best at the time of day when the species was most abundant; the significance of this is discussed.


Cnemidophorus burti is formally named, described and diagnosed. The type locality is "near La Posa, 10 mi. NW Guaymas". A photograph of the type, which is lined with no spots, is provided.

218. —. 1940. Palatal sesamoid bones and palatal teeth in Cnemidophorus, with notes on these teeth in other saurian genera. PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON 53: 119-124.

Palatal sesamoid bones and teeth are present in several species
of *Cnemidophorus* (gularis, grahamii (= tesselatus), perplexus (= ?), tesselatus (= tigris) and sexlineatus). Only the latter are present in *C. burti*.


The morphology, color and pattern of both species is described in detail. Morphometric comparisons are made; each species exceeds the other in the variability of certain characters. *C. inornatus* is, in general, the more variable of the two. The triploid parthenogenetic nature of *C. velox* suggests that intraspecific variability occurring through mutations is unlikely, and implies reorigination (multiple hybridization events). Morphological characters may diverge, converge, or both in areas of sympatry, depending on characters and samples examined. The habitat of 2 of the 3 zones of sympathy, both in New Mexico, is described; they appear to be ecotonal or disturbed in nature.


Specimens reported here occur in a mapped hiatus for the species. This paper primarily pertains to previous works by Zweifel (1962) and Dessauer et al. (1962) on intergradation between two subspecies of this lizard.


*Cnemidophorus perplexus* = *C. neomexicanus*. 2 out of over 100 lizards examined from Dona Ana County appear to be hybrids. They are compared in exhaustive morphological detail to samples of both presumed parental species from in and near the hybridization area.


The males were found in triploid populations of *Cnemidophorus exsanguis* (New Mexico), *C. tesselatus* (Colorado, New Mexico) and *C. velox* (Colorado), so they are not significant in terms of possible
sexual reproduction within these parthenoforms. It is suggested that they were derived parthenogenetically rather than being of hybrid origin. The presence of males proves that vestiges of bisexuality are retained within these parthenospecies and their scarcity may indicate that the evolution of parthenogenesis has reached an advanced stage.


It is suggested that the disjunct distribution of C. tessellatus in the west Texas panhandle is due to competition with C. tigris or C. gularis, as suitable habitat is present. The absence of males of the species in museum collections is noted. Size distribution of specimens indicates that most will not reach reproductive maturity until their second spring after birth. C. tigris marmoratus appears to be extending its range east of the Pecos River and into the caprock area below the high plains of northwest Texas. Reproductive maturity for both sexes is not reached until the second spring after birth, and the size at maturity is significantly smaller than that for C. tessellatus.


Pre- and post-test densities of Cnemidophorus tigris are given for the blast which occurred on 6 July 1962. Descriptions of the habitat, nuclear device, physical damage and radiation dosages are given. Adults were exterminated to a distance of 4000 feet from ground zero. No changes attributable to the explosion were detected beyond 8300 feet. Eggs hatched following the test in areas where adults did not survive. Immediate mortality is attributed to blast effects, delayed mortality to the destruction of habitat. Cnemidophorus may be more susceptible to deleterious effects than Uta.


Spring densities ranged from 3 to 8 lizards per acre, biomass between 43-114 gms/acre. The sex ratio was 1:1. Minimal annual adult survival was 54-60%; life spans may be as great as 7 years. Most females laid only 1 clutch per year of 2-4 eggs. Sexual maturity was normally reached during an individual's 3rd year (2nd reproductive season). The correlation between reproductive events and population...
size and structure is discussed.


Six proposed pathways of oogenesis for unisexual vertebrates are reviewed. All parthenogenetic Cnemidophorus probably (although only demonstrated for C. uniparens) form ova by suppressing cytokinesis at the last premeiotic mitosis, which is then followed by two meiotic divisions based on pseudobivalents rather than synapsed homologues. Although they are fixed heterozygotes (and thus possibly well buffered against environmental shifts), there is no evidence for great antiquity of any of the unisexual species. The addition of new genetic variation by mutation and the elimination of ill-adapted genomes by selection cannot result in sufficiently rapid evolution to enable them to survive as long as sexual species.


The key will only identify specimens that are adults, alive or freshly killed, and for which collection sites are known. Tentative range maps are included which are stated to provide a reasonably accurate estimate for each taxon. Cnemidophorus dixoni is not recognized to occur in New Mexico; that population is retained as C. tesselatus.


Cnemidophorus cf. tigris and Cnemidophorus sp. (probably sonorae) were found. A biogeographical discussion is presented in which the restriction of desert faunas to Mexican refugia during glacial periods is not supported.


The fauna includes Cnemidophorus cf. tigris and C. spp., and ex-
tends back to 11500 years B.P. Several species of Cnemidophorus (ex-sanguis, tesselatus, tigris and uniparens) are common in the present fauna of the area, but the genus is only moderately represented in the fossil fauna. The paleoecology and zoogeography of the region is discussed.


The first three criticize Cuellar for ignoring data, misunderstanding and misrepresenting facts and discussions that overwhelmingly support the hybrid origin of parthenogenetic Cnemidophorus in favor of his own theory of the spontaneous occurrence of parthenogenesis in hybrids in areas devoid of the sexual species. Cuellar replays that he did not mean to question the hybrid origin of parthenogenesis, only the assumption that parthenogenetic Cnemidophorus arose directly from hybridizations without some intervening step(s) and whether or not all hybridization events lead to successful parthenogenetic forms. The possibility of clonal succession over evolutionary time, suggested by Cuellar, is discussed.


Data for 2 different populations of Cnemidophorus tigris indicate that larger females lay more and larger eggs than do smaller females. There is evidence for multiple clutches in both populations.


Data on caloric, ash and water content of eggs and bodies of Cnemidophorus tigris, C. inornatus, C. sonorae and C. uniparens are presented. Formulae for the conversion of all other data to caloric content and the application of such data to future lizard energetic studies are discussed.


Data are presented for one activity season. The habitats with
the greatest density of vegetation had the greatest density of lizards. Daily activity periods became bimodal in the summer. Food data is summarized; individual lizards foraged at the base of vegetation and moved over a wide area. Seasonal differences in food items consumed correlated with seasonal differences in prey abundance. Roadrunners are a major predator of C. tigris. Breeding activities peaked in May and June; females produced eggs from late May until late August. Mean clutch size was 2.9 (1-5) and two clutches were produced. Fat body cycles for males, females, and immatures are discussed. The minimization of competition with sympatric lizard species (none of them teiids) by various means is discussed.


Systematic problems in this and related species are discussed. 7 subspecies are recognized. Cnemidophorus gularis gularis ranges from southern Oklahoma through Texas (and part of New Mexico) and much of northeastern Mexico. A minimum of 4 moderately distinctive morphtypes are recognized within this area, but formal recognition is deferred until further field work elucidates any significance to this relationship (from abstract).


Cnemidophorus sexlineatus viridis and 3 other lizard species were studied in Ellis County, Kansas. The habitat consisted of artificial sand pits and surrounding areas. The vegetation is described; the dominant ground cover was Buchloe dactyloides. Data on home ranges, growth rates, and habitat preferences are given for each species. C. sexlineatus viridis did not exhibit a microhabitat preference. Burrows were utilized as seasonal refuges. Lizards of this species appeared later in the day but disappeared earlier in the season than the other 3 species. A behavioral incident suggesting a thermal sensitivity to rapid temperature changes (thermesthesia) in this species is described. Food items consumed by C. sexlineatus included orthopterans (28%), lepidopterans (20%), spiders (15%), and snails of the genus Vertigo (4%); diet overlapped broadly with the other lizard species. Home ranges averaged .03 acres, but this value is not very reliable because of the methods used in determining it. Growth and reproduction are discussed. The average clutch size of 2.8 was the lowest of the 4 species in this study, but C. sexlineatus was the most numerous in the area. The data presented indicate that C. sexlineatus holds a competitive edge in this situation, which could change as the habitat reverts to natural grassland.

A complete type of tectorial membrane is found in the lizard Cnemidophorus tesselatus. A photomicrograph of the inner ear is presented and a complete description of the tectorial membrane and its relation to other inner ear structures is given.


Cnemidophorus exsanguis, C. inornatus, C. tesselatus and C. tigris marmoratus were part of a community studied in 4 habitat types of a Chihuahuan Desert watershed. C. tesselatus and C. tigris were permanent residents of open Larrea and yucca-mesquite-Ephedra habitats and transients in playa grassland habitat and arroyo shrub associations. C. exsanguis was an immigrant from montane habitats into playa grassland and yucca-mesquite-Ephedra habitats, as was C. inornatus, which was also present as a transient resident. Cnemidophorus tigris populations fluctuated markedly, showing a doubling in density in certain years. Increased rainfall and food availability resulted in larger clutch sizes, increased survivorship of hatchlings and recruitment of young into the population. Playa and bajada populations exhibited some seasonal cyclic differences; bajada population levels also tended to fall more quickly after an opportunistic increase. Cnemidophorus tesselatus populations, however, exhibited very little fluctuation in densities over the 5 years encompassed by this study, remaining at all times at a much lower level than those of C. tigris. Adults and hatchlings of both species exhibited varying degrees of allochronic seasonal activity based on food availability and abundance. The playa acts as a "cold-air sink", delaying spring emergence of lizards 3-4 weeks behind those on the bajada. Overall lizard species diversity for a given year was correlated with the previous 2 years rainfall.


Problems concerning the use of the species concept in different ways by biologists with diverging viewpoints (i.e. ecologists and evolutionists) are discussed. Simpson's definition of the 'evolutionary species' is modified to "a species is a lineage of ancestral-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate". The application of the evolutionary species concept to allopatric demes and to asexual species is discussed. It is concluded that the lack of evolutionary divergence forms the basis for grouping such populations into single species (i.e. all C. tesselatus clones belong to a single spe-
cies). It is suggested that some ecological species definitions lead to underestimations of the rate of extinction due to interspecific competition because their logical frameworks exclude unsuccessful species from being considered species.


A population in central California was studied for three years. Lizard body temperatures were closely correlated with substrate temperatures. Body temperatures of active lizards ranged from 33 to 41°C. The mean body temperature of juveniles is lower than that of adults. Seasonal activity is bimodal. The thermal characteristics of microhabitats lizards utilized were measured and correlated with lizard activity over the study period: the first year was optimal, the second too hot and the third too cold. C. tigris was more active, abundant and enjoyed higher reproductive success over the first year than over the other two. Emergence and retreat depend upon favorable thermal microhabitats and releasing subsurface temperatures of 30-33°C. Lower reproductive success was caused by high temperatures reducing favorable egg deposition sites and intraspecific interference with foraging activities during shortened activity seasons (from abstract).


Some morphological characteristics for Cnemidophorus burti sictogrammus are given. A review of diagnostic characters of C. tigris gracilis and C. tigris septentrionalis is presented and range maps (now obsolete) given.


Cnemidophorus tesselatus was collected along the Rio Florida in northern Chihuahua in vegetation of willows, cottonwoods, and fairly heavy undergrowth. C. tigris marmoratus was collected from the same vicinity.


Two specimens from the state are reported. The systematic uncertainty regarding this taxon as it pertains to confusion over the occur-
rancence of this species in New Mexico is reviewed.


These lizards are reported as sympatric sibling species in New Mexico. The nomenclatural history of each is reviewed. Morphological characteristics are compared; north-south oriented clines are present in both species. Distinguishing features are given for both species. Marked ecological differences were found: C. velox is primarily an inhabitant of oak-mountain mahogany and pinyon-juniper associations with little or no grass cover whereas C. inornatus inhabits primarily grassland associations whether primary or overgrazed and replaced by pioneer invaders.


Specific relationships between Cnemidophorus inornatus, C. uniparens and C. velox are examined. Variation in meristic characters from sympatric populations of at least 2 of the species in Arizona, New Mexico and Chihuahua is discussed. Geographic and ecological characteristics of the 3 species are discussed with particular emphasis on areas of sympathy. Four specimens representing possible hybrids between C. inornatus and C. uniparens are examined. It is concluded that the 3 forms discussed are readily distinguishable on the species level and a key is provided.


The history of application of the name is reviewed, and a recommendation of complete removal of the name from availability within the genus is made.


A summary of information on the species, including a bibliography and range map, is provided. The major part of the species' distribution is on sandy soils within the Rio Grande floodplain, where periodic flooding maintains perpetually disturbed situations. It can also be found at the edges of playas, sandy arroyos and washes, and in other
open sandy habitats.

247. —. and W. G. Degenhardt. 1962. The type locality of
Cnemidophorus perplexus. COPEIA 1962(1): 210-211.

The type locality in Sandoval County, New Mexico, is determined
through historical accounts. The area is revisited and specimens re-
ferrable to the taxon collected. The ecological history of the area
is discussed, and a map is provided. (NOTE: C. perplexus implies C.
neomexicanus but is not synonymous with it. See Lowe and Wright (1966)
and Wright and Lowe (1967b)).

248. —. and C. H. Lowe. 1965. The rediscovery of Cnemidophorus ariz-

The taxonomic history of the name Cnemidophorus arizonae Van Den-
burgh is discussed, and the lizard known by this name is formally refer-
ed to Cnemidophorus inornatus arizonae. The new species Cnemidophorus
uniparens is also formally recognized. Both taxa are described, diag-
nosed and compared with other taxa within the genus, and their geogra-
phic distributions are given.

249. —. and —. 1967a. Evolution of the alloplloid parthenospecies
Cnemidophorus tesselatus (Say). MAMMALIAN CHROMOSOMES NEWS-

The hybridization steps yielding diploid and triploid clones of
this parthenoform from C. tigris, C. septemvittatus and C. sexlineatus
are outlined.

250. —. and —. 1967b. Hybridization in nature between partheno-
genetic and bisexual species of whiptail lizards (genus Cnemidophorus).
AMERICAN MUSEUM NOVITATES No. 2286: 1-36.

Six morphologically aberrant specimens of Cnemidophorus taken
from 3 localities in New Mexico represent hybrids between the sexual
species C. inornatus and the parthenospecies C. neomexicanus. They
are morphologically identical to the type specimen of C. perplexus
Baird and Girard, and differ in the same aberrant ways from C. neomex-
icanus. They carry a triploid chromosome complement of 69, consisting
of the diploid complement of 46 from the parthenospecies and a haploid
complement of 23 from the paternal sexual species. The total hybrid
sample of 7 consists of 3 males and 4 females. A detailed morphologi-
cal analysis of the hybrids and samples of the parental species from
points of sympatric hybridization was made. The overall hybrid index for the 11 characters analyzed places the hybrids exactly intermediate between the parental forms; the hybrids resemble one or the other parent more closely when individual characters are considered. Thus C. perplexus represents an unsuccessful hybridization event in this genus spanning a period of over 100 years. The three hybrid localities (8.4 mi. W. of Hatch, Dona Ana Co; 9 mi. E. of La Joya, Socorro Co; San Pedro Creek and Tanque Arroyo, Sandoval Co.) exhibit disturbed or ecotonal habitats. A fourth hybrid locality mentioned but not reported on here is in the vicinity of Mesilla, Dona Ana County.


The parthenospecies exsanguis, flagellicaudus, neomexicanus, sonorae, tesselatus, uniparens and velox are each ecologically characterized. The primary center of distribution of these forms is the North American southwest adjacent to the Continental Divide and the area of confluence between the Rocky Mountains and the Mexican Plateau. The habitats occupied by the various species are diverse but can be defined as "weed habitats". The presence of such habitats at the time of origin of parthenogenetic individuals from hybridization between bisexual species is a critical factor and the features that contribute to the perpetuation of the parthenospecies are discussed.


Nine species from Nevada, including Cnemidophorus tigris, were studied. At least 6 different acids were present in this species, with cholic acid being the primary one. Teiids and Gekkonids had very similar compositions.


Morphological and distributional attributes of Cnemidophorus tigris marmoratus are discussed.

Fertile hybrids between _C. t. gracilis_ and _C. t. marmoratus_ are described from an area 45 by 65 miles centered on the northern Animas Valley in southwestern New Mexico. Evidence for hybridization is based on color and scutellation characteristics. The ecological distribution of the two subspecies within the study area is described. Hybrids are known from 3 areas; Granite Gap and Steins in the Peloncillo Mountains and in the vicinity of Redrock. The hybrid zone in the Peloncillos is only about one mile wide. Historical factors presumed to influence the described phenomenon are discussed. It is suggested that the two subspecies came into contact during post-Wisconsin times due to the establishment of a desert corridor across the Continental Divide along with expansion of the two taxa from glacial refugia. They are so similar in habitat requirements and adaptations that neither is replaced by the other. Hybrids are produced because of the absence of reproductive isolating mechanisms but hybrid gene combinations are selectively disadventagous compared to pure parental types.


This is the classic paper on the species. Its unisexual nature is confirmed, and individual and geographic morphological variation is described in detail. A range map is given. Six pattern classes are described, with greater amounts of ontogenetic change in pattern occurring from class A through class F. Pattern classes C and D occur in northeastern New Mexico, sometimes sympatrically, northeast of the Pecos River. Pattern class E occurs throughout the rest of the state, except for two isolated populations in Hidalgo County which are referable to pattern class F. There are places throughout the range of E, for instance Socorro County, where adjacent populations are morphologically different. The existence of multiple clones is suggested. No geographic trends are apparent; variation appears to be random. Variation in 3 scale characters tends to separate classes A-D from E and F. The most striking feature of variation is the relative homogeneity of lizards of class E (geographically the most widespread class) and the diversity of populations occupying the minor remaining part of the species range. _C. tesselatus_ shows ranges of variation in pattern and scutellation quite similar to those of widely distributed sexual species of the genus. When samples from restricted areas are compared, however, _tesselatus_ usually exhibits much less variation than the sexual _C. tigris_.

Patterns of evolution in _C. tesselatus_ are discussed. The apparent absence of multiple clones in most local populations is attributed to low mutation rates and/or strong selection for the best-adapted clones to local conditions. Advantages of parthenogenetic reproduction include a higher intrinsic population rate of increase compared with a similarly structured sexual population. A parthenogenetic population consisting of one or a few similar clones that were particularly well-adapted to existing conditions might have an advantage over a sexual population that, in effect, sacrificed some of its offspring in
more frequent deleterious gene recombinations. But if the parthenogen could not respond quickly enough by genetic adaptation to changing environmental conditions, the population might be at a disadvantage compared to a sexual one able more readily to draw upon stored genetic variation. It is suggested that parthenogenetic populations may depend upon, and be able to tolerate, greater mutational rates than sexual populations. There is no evidence that parthenogenetic Cnemidophorus exhibit a wider ecological valence than sexual species, which could compensate for lower populational potential for genetic change. Pattern type relationships indicate that C. tesselatus spread from north to south whereas paleoclimatic data indicate just the opposite. The northern part of the species range must have been occupied by it after the termination of Wisconsin glaciation. It is suggested that tesselatus is closely related to C. tigris or C. sejtemvittatus, or some other species in the tigris-sexlineatus complex.

Difficulties in the taxonomic treatment of parthenospecies are briefly discussed. It is suggested that the most reasonable taxonomic choice is to group all of the populations of C. tesselatus into one species; this emphasizes their presumed close relationship and common ancestry. Lizards found at the type locality today belong to class A (which is now known to be triploid) whereas the description of the type material collected in 1820 is of lizards belonging to class D (which is diploid). The closest approach of class D to the type locality today is 70 airline miles to the southeast, and class B (triploid) occupies the intervening area. A diagnosis of C. tesselatus is provided. Habitat is discussed briefly but not well defined. The species is usually but not always found on rocky soils and in roughland habitats from 1500 to 5500 feet in elevation. Its distribution is spotty throughout its range and appears to be riparian to a great extent. The habitat of the isolated population in Antelope Pass, Hidalgo County, New Mexico, is described in more detail. It inhabits a sandy desert wash dominated by mesquite and desert willow.