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## Reproduction of *Cnemidophorus inornatus* and *Cnemidophorus neomexicanus* (Sauria, Teiidae) in Northern New Mexico<sup>1</sup>

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### INTRODUCTION

The little striped whiptail lizard, *Cnemidophorus inornatus* Baird, and its close parthenogenetic relative the New Mexico whiptail lizard, *Cnemidophorus neomexicanus* Lowe and Zweifel, occur sympatrically in many places along the Rio Grande Valley of New Mexico. For the present study these species were investigated where they occur sympatrically and their reproduction was compared with the intention of determining whether reproductive processes provide one species with a competitive advantage over the other. Unfortunately, even the most exhaustive studies, such as those by Blair (1960) and Tinkle (1967) are not complete enough to allow comparisons that would permit us to conclude that one species has an over-all advantage over another. Although the number of factors that may be limiting is very large for any population, the present investigation considers only a few. The emphasis is on those factors relating to reproduction in order especially to gain some insight into the advantages and disadvantages of parthenogenesis in competing populations.

Reproduction of *C. inornatus* and *C. neomexicanus* was studied from

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September, 1965 to September, 1968. Field studies were conducted from February, 1966 to March, 1968 in two areas within the city limits of Albuquerque. The lizards are sympatric in both areas.

Medica (1967) briefly studied the life history of these and several other species of *Cnemidophorus*. His investigation was made approximately 200 miles south of the present study areas, and his data are compared with mine whenever possible. My findings are also compared with those from published works on other species of the family Teiidae, including Fitch (1958) on *C. sexlineatus*, McCoy and Hoddenbach (1966) on *C. tigris*, Bostic (1966) on *C. hyperythrus*, and Smith (1968) on the tropical teiid *Ameiva quadrilineata*. An attempt is made to correlate my work with many life-history studies of representatives of other lizard families.

Few genera have been distinguished by the amount of taxonomic confusion that is still characteristic of *Cnemidophorus*. Fortunately, the populations to which the names *Cnemidophorus inornatus* Baird and *C. neomexicanus* Lowe and Zweifel are correctly applied are now reasonably well defined. Current synonymy of *C. inornatus* with comments on the taxonomic history of the species is given by Axtell (1961) and Wright (1966). Problems concerning the type locality of *C. neomexicanus* were settled by Maslin, Biedleman, and Lowe (1958) and Wright and Degenhardt (1962). Lowe and Zweifel (1952), Axtell (1966), and Wright and Lowe (1967) gave synonymies and comments on the taxonomic history of this species.

In general terms, the range of *C. inornatus* extends from extreme south-eastern Coahuila and adjacent Nuevo Leon through western Texas and all but northeastern New Mexico, wherever suitable desert grassland or desert shrub habitat exists. *Cnemidophorus neomexicanus* is found only along the Rio Grande Valley from approximately 100 miles southeast of El Paso, Texas to Santa Fe, New Mexico, primarily in lowland areas disturbed by overgrazing or erosion. There is an isolated population near Lordsburg in Hidalgo County, New Mexico. Up-to-date accounts of the geographic distribution of *C. neomexicanus* were given by Taylor (1965), Axtell (1966), and Wright (1966). The distribution of *C. inornatus* was given by Axtell (1961).

## MATERIALS AND METHODS

Field studies of *Cnemidophorus inornatus* and *C. neomexicanus* were conducted from February, 1966 to March, 1968. Study areas containing sympatric populations of the two species were located within the Albuquerque city limits in open fields at the intersection of Gibson Boulevard and San Pedro Drive and on both sides of Central Avenue on the east side of

Eubank Boulevard. Field observations were made and specimens obtained for laboratory investigation from these areas and from foothills due east of Albuquerque on the west side of the Sandia Mountains, as well as from other open areas within the Albuquerque city limits.

From the above localities 1020 specimens were obtained, of which 916 were collected during the investigation, and 104 were obtained from collections already in the Museum of Southwestern Biology. Although all these specimens were used in some phase of the study, most of those used in analysis of reproduction were drawn from 428 *C. inornatus* and 346 *C. neomexicanus* which I collected, preserved, and catalogued. The remaining specimens were kept in captivity for hormone studies or used for comparative material.

Observations of activity periods, behavior, and habitat selection of lizards in the study areas were made and recorded. Observations and collections were irregular during April and October because inclement weather apparently limited above-ground activity of the lizards. With few exceptions, weekly collections were made throughout May, June, July, August, and September. Lizards were collected alive whenever possible by hand and often with the help of drift fence traps or rubber bands. Hibernating lizards were obtained by digging.

All specimens used in calculations were dissected, and sex was determined by gonadal examination even though sex of adults could, in many cases, be determined on the basis of secondary sexual characteristics.

Specimens were usually dissected and examined the day following collection, but occasionally they were frozen for examination later. All measurements were made prior to fixation except for the few specimens already in the museum collection. Specimens were tagged, fixed in 10 per cent formalin, subsequently preserved in 55 per cent isopropyl alcohol, and deposited in the Museum of Southwestern Biology at The University of New Mexico.

Weights and linear measurements were taken of whole lizards as well as of various reproductive organs. All linear measurements were made in millimeters with vernier calipers. Snout-vent length was measured from tip of snout to anterior lip of vent to the nearest millimeter. All other gross measurements (of eggs, ovarian follicles, testes, and head) were made to the nearest tenth of 1 millimeter. Cell and tissue measurements were made to the nearest 10 microns with an ocular micrometer. All weights were made only with fresh lizards having complete unregenerated tails and were made on analytical balances. Whole specimens were weighed to the nearest milligram, but organs were weighed to the nearest tenth of a milligram. Epididymides and vasa deferentia were not separated,

hence each set was weighed as a single unit. These, fat bodies, and oviducts were not usually weighed directly except in hormone studies, which are presented in another paper, but were assigned arbitrary numbers roughly equivalent to those given to preweighed standards. Calculations involving cyclic changes in these organs were based on the assigned numbers rather than exact weights. Likewise, lizard color was recorded as numbers equivalent to numbered standards, and calculations were made with these numbers.

Testes, ovaries, epididymides, and oviducts were prepared for histological examination. These tissues were fixed in buffered 10 per cent formalin, embedded in paraffin, and sectioned at 5 or 8 microns. Most sections were stained with Schiff's leucofuchsin stain and counterstained with light green, but a few were stained with Harris's hematoxylin and counterstained with eosin. More than 300 permanent slides of these tissues were prepared and representatives were placed on file in the Museum of Southwestern Biology. In addition to these slides, many squashes of testes and epididymides were made to test for presence of sperm. These were usually stained with methylene blue and were not kept for permanent record.

Measurements and other raw data were recorded on separate cards for each lizard. Means, standard deviations, and standard errors for most samples were calculated with an IBM 360 Mod. 40 computer at The University of New Mexico Computer Center. Confidence limits (95%) were also calculated on this machine, although many of these as well as periodic checks and other calculations were made with an Olivetti-Underwood tape read-out calculator.

## RESULTS AND DISCUSSION

### INTERSPECIFIC RELATIONSHIPS

*Cnemidophorus inornatus* and *C. neomexicanus* occur sympatrically at the two main study areas. Both species were encountered several times as the investigator walked across the study areas. A closer analysis, however, showed that the species have well-defined ecological preferences which largely prevent their intermingling.

**SPECIES COMPOSITION OF POPULATIONS:** All lizards taken at the Gibson and San Pedro study area were *Cnemidophorus*. Of these, 69 per cent were *C. inornatus* and 31 per cent were *C. neomexicanus*. At the Eubank and Central study area *Holbrookia maculata*, *Uta stansburiana*, and *Phrynosoma douglassi* were also collected. In this area, which is less disturbed than Gibson and San Pedro, 80 per cent of the *Cnemidophorus* taken were *C.*

*inornatus* and 20 per cent were *C. neomexicanus* (see table 1). The latter lizards were all collected along road banks, ditches, or near piles of man-made trash.

**HABITAT PREFERENCE:** *Cnemidophorus inornatus* is found in or around ungrazed areas of dense grass and short herbaceous weeds in the Albuquerque area. The terrain is typically flat or gently sloping and generally free of such obstructions as large *Dipodomys* burrows, large shrubs, trees, or piles of trash. Occasionally, individuals are seen foraging in small areas with less vegetation, but they rarely stray more than a few feet from cover. At the approach of an intruder, the lizard immediately runs toward cover, usually a dense clump of grass.

The habitat of *C. neomexicanus* contrasts sharply with that of *C. inornatus*.

TABLE 1  
RELATIVE NUMBER OF ADULT *Cnemidophorus inornatus* AND *C. neomexicanus* FROM TWO  
MAJOR COLLECTING LOCALITIES

Locality	Total Specimens	<i>C. inornatus</i>		<i>C. neomexicanus</i>	
		No.	%	No.	%
Gibson and San Pedro	352	244	69	108	31
Eubank and Central S. E.	199	159	80	40	20

The parthenogenetic species generally occupies sparsely vegetated disturbed areas. These lizards are most numerous around piles of trash, loose dirt at the edge of roads and ditches, and at the base of large weeds, shrubs, and trees, and are often the only lizards found in very heavily grazed areas. An occasional individual was seen running through grass to escape an intruder, but I observed no instance of an adult *C. neomexicanus* foraging in heavy grass.

The present study certainly supports the hypothesis that *C. neomexicanus* flourishes in areas recently disturbed by man and that when this disturbance destroys native grassland it is frequently at the expense of *C. inornatus*. These observations give added evidence to the conclusion by Wright and Lowe (1968) that "With continued disturbance accented more and more recently by the activities of man and his animals, the geographical range of *C. neomexicanus* appears to be expanding and this also appears to be at the expense of *C. inornatus*."

Special attention was paid to incidences of contact between lizards in order to postulate the importance of direct competition between the species (e.g., direct competition in the sense of physical or visual contact).

Often during the study individuals of both species were driven into the same drift-fence trap at the same time. Generally the lizards appeared not to recognize each other as animate objects, and in many cases they climbed over one another. In only one instance was a lizard of one species observed to react to the presence of another lizard in the field. This occurred along a wall on the south side of the Gibson and San Pedro study area in June, 1967. There, an individual of *C. inornatus* was driven from a grassy area to the wall. As it ran along the wall, it suddenly found itself about 5 inches from a large individual of *C. neomexicanus*, which immediately lunged at it and ran about 2 feet after it.

In the laboratory we observed many instances in which individuals of *C. neomexicanus* attacked those of *C. inornatus*. When several individuals of each species were placed in a single terrarium, as many as half of the *C. inornatus* lizards were killed. In these terrariums large *C. neomexicanus* individuals were frequently seen biting smaller adults of *C. inornatus* on the head. Almost without exception, dead specimens of *C. inornatus* that were removed from these cages had dried blood around the nose and mouth. Individuals of *C. neomexicanus* were seen biting other lizards (but rarely smaller individuals of the same species) on the neck and tail. I did not observe an instance in which individuals of either sex of *C. inornatus* attacked individuals of *C. neomexicanus*. The aggressiveness of the latter species toward the former may be a behavioral factor that tends to prevent mixing of the species in nature.

The separation of species resulting from their habitat preferences and other behavioral differences were seen to break down under one general circumstance. This involved situations in which the two habitats came into immediate contact usually as a result of man-made hedges, fences, or roadbeds cutting into typical habitat of *C. inornatus*. It was in these situations that the hybrids reported by Christiansen and Ladman (1968) and Christiansen, Degenhardt, and White (In press) were found. The existence of these hybrids gives evidence of the most intimate form of interspecific contact.

#### RATIO OF MALES TO FEMALES

Of the 428 specimens of *C. inornatus* of all age groups used for gonadal studies, 214 were males and 214 were females. As these specimens were chosen at random and were the product of normal daily collections, the exact 50-50 ratio was surprising. The sex ratio was 191 (51.3%) males to 181 (48.7%) females for 372 adults, whereas corresponding figures for 56 juveniles of *C. inornatus* used in the study were 23 (41.1%) males to 33 (58.9%) females. Tinkle (1961) noted large differences from an expected

50–50 ratio in populations of *Uta stansburiana*, and Christiansen (1965) found that similar differences in another population of *Uta stansburiana* were due to sampling error resulting from behavioral differences between the sexes. In the present study, no differences in behavior of the sexes on the ground surface were noted. It was apparent, however, that during the early months of the year (April, May, and June) more adult males of *C. inornatus* were seen and collected than adult females (82 males and 42 females) but in the latter part of the year (July, August, and September) the reverse was true (109 males and 139 females were collected). The sparsity of females during the early months is judged to be due to unobserved behavioral differences related to the formation and laying of eggs during this period. For instance, the activity of laying eggs requires that the female be under cover and possibly underground. No reason is known why males would be underground while females would be on the surface. Also, the brighter blue coloration of males in spring might make them more visible.

It is well established that *C. neomexicanus* are all female (see Maslin, 1962, 1966; Taylor and Medica, 1966; and Wright and Lowe, 1967). All 203 adults and 68 juveniles of *C. neomexicanus* that underwent gonadal examination in the present study were females.

#### GROWTH AND ATTAINMENT OF SEXUAL MATURITY

Within the present text a lizard is referred to as an adult if it has attained reproductive maturity (i.e., is capable of producing gametes during the reproductive season). Individuals that have not attained reproductive maturity are referred to collectively as juveniles even though they may vary in size from the smallest hatchlings to individuals of nearly adult size. The term "hatchling" refers to juveniles that hatched in the same calendar year in which they were collected, whereas the term "subadult" refers to those juveniles that are in their second calendar year of life.

Size at maturity was determined from specimens captured during the reproductive season (primarily April, May, and June) at which time differences between mature and immature gonads were most evident. Presence of enlarging ovarian follicles with yolk (i.e., possessing a definite yellow color as opposed to white), oviducal eggs, or corpora lutea were the criteria for maturity of females. Presence of spermatozoa was the criterion for adult males.

The smallest male of *C. inornatus* possessing sperm was 49 mm. long, hence specimens of this snout-vent length or longer were considered adults. Some smaller specimens demonstrated testicular enlargement dur-

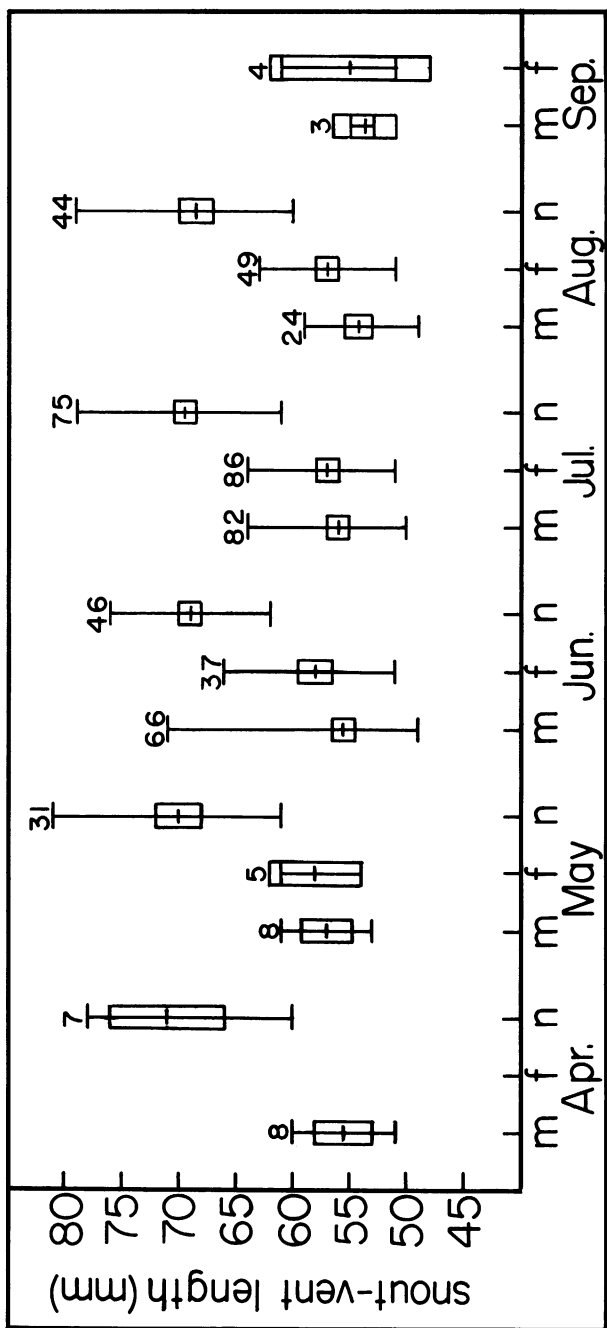


FIG. 1. Snout-vent lengths of adults of *Cnemidophorus inornatus* and *C. neomexicanus* used in analysis of reproduction. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

Abbreviations: m, *C. inornatus* males; f, *C. inornatus* females; n, *C. neomexicanus*.



ing the reproductive season but none was observed to contain spermatozoa. The smallest female containing enlarged follicles had a snout-vent length of 51 mm., and this was considered the minimum size of an adult female of *C. inornatus*. All specimens containing oviducal eggs or corpora lutea were larger. Males of *C. inornatus* ranged from 49 to 71 mm., whereas females ranged from 51 to 66 mm. Hereafter, the term "length" refers to snout-vent length.

The smallest specimen of *C. neomexicanus* possessing enlarged follicles was 60 mm. long, hence all individuals of this species of this length or longer were considered adults. The largest specimen collected was 82 mm. long. Mean lengths of adult males and females of *C. inornatus* and *C. neomexicanus* adults for each calendar month of the two-year study of reproduction are shown in figure 1. This figure demonstrates that *C. neomexicanus* is consistently longer than *C. inornatus* and that within species no significant variation in length with month of collection was observed.

Data on the seasonal incidence of adults and juveniles are given in table 2. Hatchlings of *C. inornatus* were first observed in mid-July in 1966 (none was observed until September, 1967, possibly because of severe drought that year). Thereafter they were present in the population in increasing numbers until hibernation. The earliest hatchlings of that species collected ranged from 30 to 32 mm. in length. Even though hatching was taking place as late as September, 1967, most hatchlings had grown to 36 mm. or more by that time. June collections contained several specimens of 45 to 49 mm. but some specimens were as small as 38 mm. The incidence of subadults in June and July was low, which may indicate that some fast growing, early hatching specimens attained adult size during the early summer months following hatching, thereby appearing in those samples as adults (see table 2), but it could also be the result of a sampling error caused by what appeared to be greatly increased above-ground activity of adults. As there was no indication that hatchlings grew as much as 7 mm. during the period between hatching and hibernation, few specimens could be expected to grow another 10 to 12 mm. during the three spring months following hibernation, which would be necessary for them to reproduce that year. It is my opinion, therefore, that very few if any specimens reproduce during the year following hatching. This opinion is supported by the fact that two hatchlings of *C. neomexicanus* and one of *C. inornatus*, which were kept in the laboratory and fed well from August 20 to May 30 were substantially smaller than adult size by May 30. If any do achieve adult size, they might be expected to be males, which mature at a smaller size than females.

The first *C. neomexicanus* hatchlings appeared in the last two weeks of

July, 1966 but not until the first two weeks of August, 1967. The smallest of these ranged from 37 to 38 mm. long. All juveniles of this species had attained lengths of at least 41 mm. by spring. By August all subadults of *C. neomexicanus* had grown to a length of 50 mm. or more. It is likely that most, if not all, of these would be reproductively mature by the following June, which would be their third calendar year of life. Some specimens probably reach adult size by August of their second calendar year, but it does not seem likely that any would mature in time to reproduce that year.

#### THE ANNUAL CYCLE OF ACTIVITY AND HIBERNATION

Surface activity of both species begins in April. The earliest collected *C. inornatus* individual was a male taken on April 14, and the earliest of *C. neomexicanus* was taken on April 1. Males of *C. inornatus* tend to emerge earlier and are much more active than females during April. Observations also verified the fact that juveniles were more active during that month than were adults of either species. These observations support those made by Medica (1967) in southern New Mexico indicating that immature individuals of *C. inornatus*, *C. neomexicanus*, *C. exsanguis*, and *C. tigris* appeared in the spring before the adults did. Other workers have had similar findings. There was also some indication (table 2) that *C. neomexicanus* individuals began surface activity before females of *C. inornatus* did.

The populations of both species contained the highest percentage of adults and the lowest percentage of juveniles in July. The proportion of adults declined rapidly after that until October, when no adults were

TABLE 2  
RELATIVE NUMBERS OF JUVENILES AND ADULTS OF *Cnemidophorus inornatus* AND  
*C. neomexicanus* COLLECTED IN THE REGION OF ALBUQUERQUE DURING 1966 AND 1967

Month	<i>C. inornatus</i> Males			<i>C. inornatus</i> Females			<i>C. neomexicanus</i>		
	% Adult	% Juvenile	Total No.	% Adult	% Juvenile	Total No.	% Adult	% Juvenile	Total No.
April	67	33	12	0	100	4	44	56	16
May	67	33	18	21	79	14	46	54	26
June	94	6	66	91	9	47	69	31	67
July	93	7	81	94	6	85	81	19	110
August	72	28	36	81	19	67	76	24	38
September	57	43	7	29	71	14	25	75	4
October	0	100	1	—	—	0	0	100	1

seen in the field. The last adults of the two species were seen and collected in the third week of September although occasional juveniles were observed in the field until the first week of October. The disappearance of adults from lizard populations in the fall has been observed by many workers, among them Carpenter (1959) with *C. sexlineatus*, Milstead (1957) with *C. inornatus*, and Medica (1967) with four species of *Cnemidophorus* including the two considered in the present study. Bostic (1966) reported that adults of *Cnemidophorus hyperythrus beldingi* in southern California "usually enter into hibernation in late July through most of September, and immatures in December." The stimulus responsible for the cessation of surface activity of some individuals while others continue is not known. A useful investigation might involve a study to determine whether the need to acquire additional fat for hibernation is responsible for later surface activity of some individuals, especially juveniles.

#### REPRODUCTIVE CYCLE OF MALES OF *Cnemidophorus inornatus*

The information in this section is based on examination of gonads from 214 males, of which 191 were adults and 23 were juveniles. The number of specimens examined each month is indicated in figure 1. Testes and epididymides from 17 adult lizards of near average size and weight obtained in seven different months were sectioned for histological study. Permanent slides were prepared from all of these specimens and are available for March, April, May, June, July, August, and September. Smears were prepared periodically to check for presence of spermatozoa and other spermatogenic stages. Photomicrographs of representative stages of the spermatogenic and epididymidal cycles are shown in figure 2. Approximate measurements of epididymides and fat bodies were made in order to gain an indication of the ways in which these tissues are related to the testicular cycle. The testes of five juveniles were examined histologically.

**SIZE AND WEIGHT OF TESTES:** Testicular size is expressed as maximal diameter in figure 3. Small testes are nearly spherical, whereas large ones are elliptical, nearly twice as long as wide. Because of the irregularity of testicular shape, weight probably provides a more accurate measure of testicular mass than does length.

Examination of gonads revealed the right testis to be consistently farther anterior than the left in both juveniles and adults. The right testis usually appeared to be larger than the left but this difference proved to be significant with 95 per cent confidence limits only for August specimens. Muliak (1946) made corresponding observations on position and

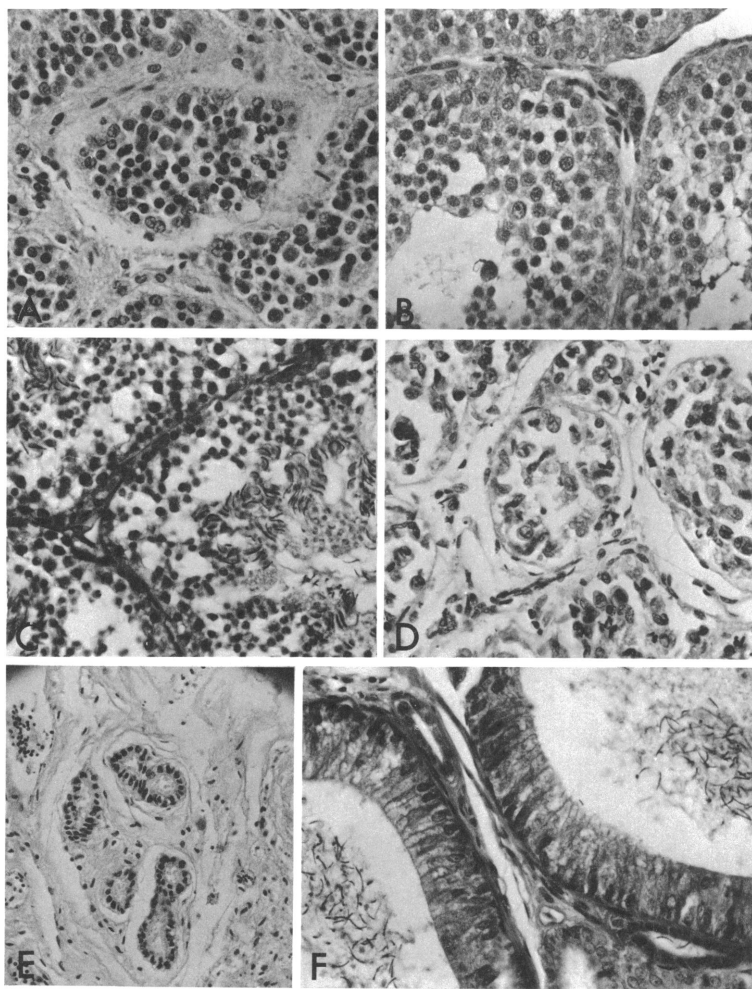


FIG. 2. Histological sections of male reproductive organs of *Cnemidophorus inornatus* adults from northern New Mexico. A. September testis (JLC 2555) showing beginning of spermatogenesis in fall. Note numerous spermatocytes and relatively thick tubule walls.  $\times 320$ . B. March testis (JLC 2659) showing condition of hibernating specimens shortly before emergence. Note numerous spermatocytes and thick tubule walls.  $\times 320$ . C. April testis (JLC 1348) showing condition at approximate time of maximum sperm production.  $\times 320$ . D. Early August testis (JLC 1721) showing maximum state of degeneration following the reproductive season.  $\times 320$ . E. August epididymis (JLC 1721) showing shorter, now more cuboidal, epithelial cells and absence of spermatozoa in tubule lumen.  $\times 320$ . F. April epididymis (JLC 1348) showing tall columnar epithelial cells and large mass of accumulated spermatozoa.  $\times 320$ .

JLC numbers are the author's personal catalogue numbers. The specimens have been deposited for cataloguing in the Museum of Southwestern Biology at the University of New Mexico.

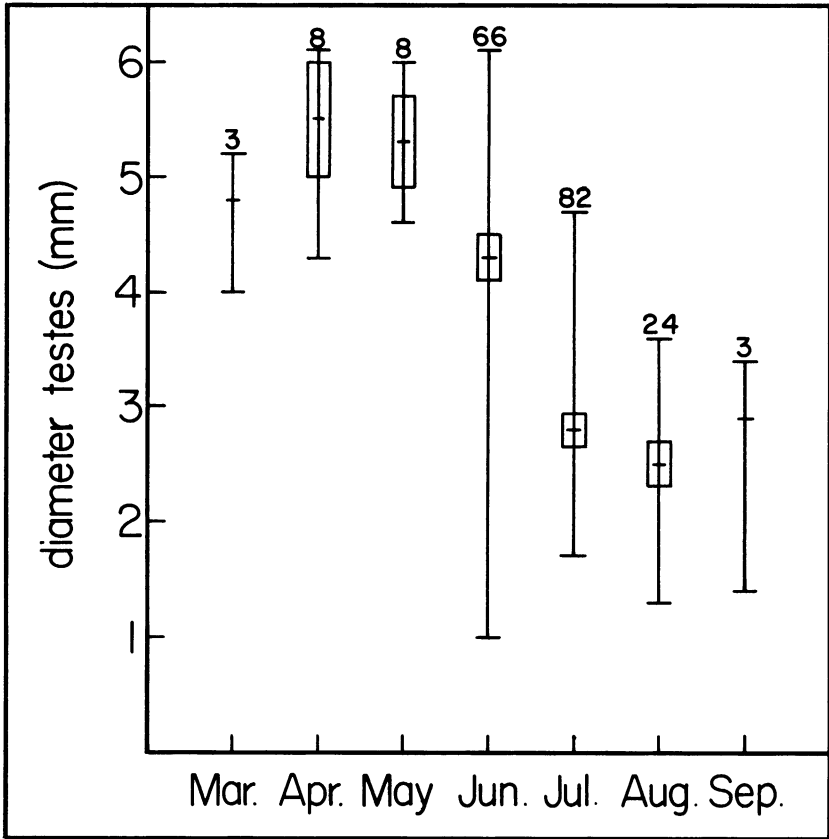


FIG. 3. Maximum testicular diameters of specimens of *Cnemidophorus inornatus* from northern New Mexico. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

relative size of testes of three species of *Sceloporus* but Bostic (1966) found no significant difference between right and left testes of *Cnemidophorus hyperythrus beldingi*.

The testes of mature males begin to enlarge in late August and September, having regressed to minimum size (fig. 3) and weight (fig. 4) shortly before. This initial autumnal increase of testicular mass is here regarded as the beginning of the male reproductive cycle. Maximum size and weight are attained the following spring immediately prior to the period of most active mating. Thereafter (from the end of May to August)

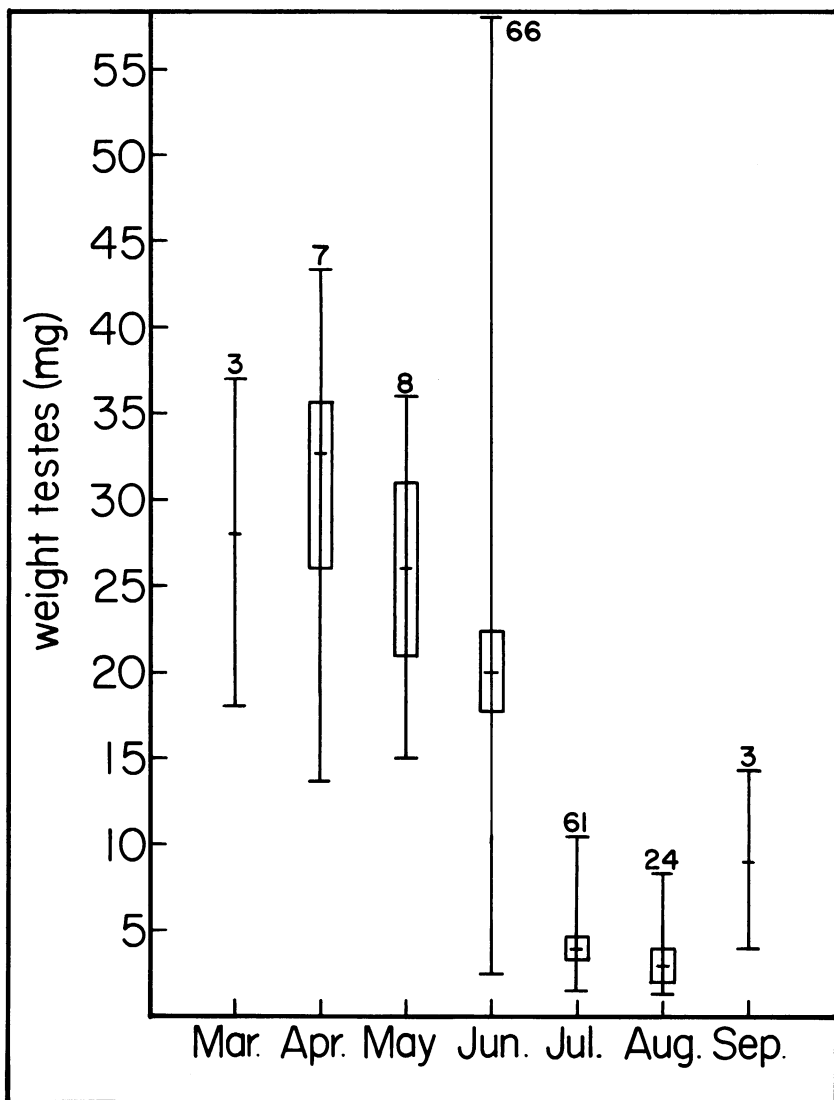


FIG. 4. Testicular weights of specimens of *Cnemidophorus inornatus* from northern New Mexico. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

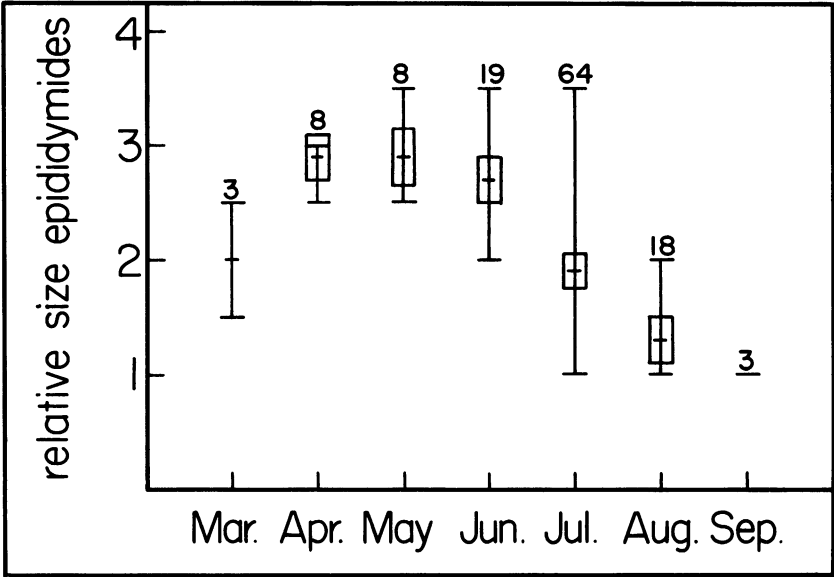


FIG. 5. Relative size of epididymides in specimens of *Cnemidophorus inornatus*. Numbers on vertical axis were arbitrarily assigned with the largest numbers representing the thickest and most convoluted epididymides. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

the testes regress, reaching minimal size and weight in August. Average weight of testes in April was 32.9 mg. (range 13.5 to 43.3 mg.), whereas the mean weight for August was 3.3 mg. (range 1.2 to 8.2 mg.). These figures demonstrate the general magnitude of regression that occurs during the summer.

The testicular regression is paralleled by a gross regression of the vasa deferentia and epididymides. Figure 5 reflects change in the relative length and thickness of these organs and shows a considerable decrease for the months of July and August. In August and September the vasa deferentia and epididymides were thin and translucent, whereas those from April and May were thick and opaque. These changes appear to be due mostly to changes in the size of the columnar epithelial cells lining the lumina (see fig. 2). Hemipenes appear to follow a cycle similar to that of the vasa deferentia. When everted they appear to be about twice as large in the spring as they are in the fall.

An interesting area for speculation concerns the increase in testicular

size and weight during the winter period of inactivity. The average testicular weight in September for three adult males was 8.8 mg. which was more than twice that of the August mean. Three hibernating adults removed from their burrows in March had a mean testicular weight of 28 mg. or about 3.5 times the September measurement. The earliest nonhibernating specimens were collected in April and had testes four times the September weight. Even considering the small sample sizes for September and March, it is apparent that some testicular growth took place during the winter months while the lizards were underground and not exposed to light. This growth is graphically shown in figures 3 and 4. Whether this growth occurs during hibernation or when the lizard might be inactive underground, but not truly hibernating, is not known.

**SPERMATOGENESIS:** The cycle of spermatogenic activity corresponds well to the cycle described for testis size and weight. The small testes of specimens in July and early August exhibit a low spermatogenic activity, in which the seminiferous tubules are collapsed and their lumina contain only cellular debris. Figure 2 shows that the seminiferous tubules contain only spermatogonia and an occasional primary spermatocyte. Most of the cells present a somewhat collapsed appearance rather than the full, more turgid appearance of similar cells earlier in the year, and seem to be in the process of exfoliation and degeneration. No spermatozoa were found after August 5 either in testes or epididymides.

Sections from specimens collected in the last week of August and in September demonstrate thickening of the tubule walls which corresponds with the increase in weight noted previously. At that time, the walls range from two to four cell layers thick and the tubules appear less collapsed than in early August, although they are still oval-shaped rather than circular in cross section. The first layer of cells consists mostly of spermatogonia, whereas the remaining layers are composed of occasional spermatogonia mixed with spermatocytes. The lumina are small and empty of cellular debris and no traces of sperm remain in the epididymides.

The spermatogenic activity initiated in the fall continues at least part of the time that the lizards are underground during the winter months. Virtually all this activity was accounted for by the accumulation of cells representing various spermatogenic stages. A small amount of growth probably resulted from an observed increase in interstitial cell size.

Testes of the hibernating adults contained all stages of spermatogenesis except mature spermatozoa. Secondary spermatocytes were the most numerous cells present, but primary spermatocytes and spermatids were also present in large numbers. Spermatogonia were at least as numerous



as they were in late fall individuals. The seminiferous tubules usually did not possess lumina and appeared as a solid mass of cells, mostly spermatocytes and spermatids, with the most advanced spermatogenic stage toward the center (see fig. 2).

Sections from two individuals taken in April, shortly after the lizards emerged from hibernation, show the seminiferous tubules to be nearly round in cross section, to have distinct lumina in at least half the tubules, and to have walls two or three times as thick as the diameters of the lumina they surround (fig. 2). These testes had the highest average weight obtained for any month during the study. The diameters of the seminiferous tubules were larger than those for any other month, and this was reflected in the testicular length (see fig. 3).

All spermatogenic stages were present during April and the walls of the seminiferous tubules contained 10 to 15 or more layers of cells. Spermatids and secondary spermatocytes were the most common spermatogenic stages present, although mature spermatozoa were present in about half the seminiferous tubules. Epididymides contained varied amounts of mature spermatozoa, but the spermatozoa were fewer than in May and June specimens.

A *t*-test using a pooled variance showed that the decrease in size and weight of testes in May was not significant within 95 per cent confidence limits. Hence, the possibility that testicular weight loss does not begin until the end of May or June must be recognized. It is my opinion that even though some late-maturing or late-emerging adults might be attaining maximum testicular development during that time, testes of most individuals are decreasing in size. This is because the proportional number of seminiferous tubules per testis full of spermatogenic elements (i.e., containing no lumina) was considerably smaller in May than in the preceding month. The tubule walls contained fewer layers of cells than they did in April, the range being from seven to 12 layers per wall (fig. 2). In May, all tubules possessed mature or nearly mature spermatozoa, and the epididymides were swollen with clumps of spermatozoa resulting from evacuation of these elements from the testes.

For the months of June and July the thickness of the tubule walls decreases steadily as spermatids metamorphose into sperm and are passed into the lumina and thence to the epididymides. By mid-June, primary spermatocytes are few and by mid-July only a few secondary spermatocytes remain. The tubule walls of most testes from June specimens ranged from four to seven cell layers thick and those from July specimens ranged from one to four. In both of these months, spermatozoa were the most prevalent spermatogenic stage present. Seemingly, there is an increasing

rate of metamorphosis of sperm from March to the end of May. If a "peak" in the amount of spermatozoa available for reproduction is reached, it is probably in the end of May or in the first week of June. Thereafter, sperm appear to be evacuated from the epididymides more rapidly than they are produced.

By the end of July few sperm are visible in the tubules and the number in the epididymides is also reduced. The tubule walls consist of spermatogonia and a few secondary spermatocytes with an occasional patch of spermatids. Possibly some metamorphosis of spermatocytes occurs beyond this point, but most spermatocytes are probably destined for degeneration and exfoliation without undergoing further division. The most regressed testes of this period show evidence of collapsing and the lumina of the tubules contain exfoliated cellular debris.

The seminiferous tubules regress to a minimal stage that is reached during the last week of July or the first two weeks of August, at which time size and weight are also minimal. The tubules are collapsed and spermatogonia are the only recognizable spermatogenic elements present in the walls. Ragged appearing cells and clumps of cells can be seen in the lumina of the tubules and in various stages of exfoliation from the walls (fig. 2). Only a few sperm remained in the tubules during the last week of July and none was visible at the end of the cycle in mid-August. Shortly after this time, proliferation and restratification of the tubule walls mark the initiation of a new spermatogenic cycle.

Smears of epididymides and vasa deferentia revealed the presence of mature sperm from April through July, the number increasing until the end of May or early June and decreasing from the end of June through July. No sperm were found in smears made from specimens taken in August or September, and the hibernating March specimens contained only immature sperm (i.e., with thick heads and short tails). Sperm were sparse beyond the second week of July, and it seemed unlikely that their number would be sufficient to effect a fertilization after that time.

**FAT BODIES AND THEIR RELATION TO THE TESTICULAR CYCLE:** *Cnemidophorus inornatus* and *C. neomexicanus* store fat in abdominal bodies of similar shape that protrude anteriorly into the coelom of the pelvic region. These fat bodies varied in males of *C. inornatus* from less than 1 mg. to 111 mg. and their weights were roughly proportional to their lengths.

At the initiation of the study, a series of fat bodies of varying sizes were removed from the lizards, measured, and weighed. They were then placed in groups numbered from one to four in order of increasing weight. Thenceforth, any fat bodies found during the study were assigned the number of the group to which they were judged to be most similar in

size. When one appeared to be intermediate between two groups, it was assigned a number which was intermediate to the numbers of the two groups (i.e., when a fat body was found to be intermediate in size between groups three and four, it was assigned the number 3.5). When a lizard without clearly visible fat bodies was found, the number 0 was recorded. These numbers were then averaged for each one-month period of the study and treated statistically to determine whether they demonstrated meaningful cyclic changes.

Males of *C. inornatus* that emerged from hibernation in April contained some fat, but the average fat content during this month was less than during any other (see fig. 5). Fat bodies remained small until mid-June at which time they began to grow, attaining maximum size at the end of June, July, or August. The three September specimens also had large fat bodies as did two of the three specimens removed from hibernation in March.

The above data demonstrate that fat deposition did not begin until the bulk of spermatogenesis had ceased in mid-June. The hibernating March specimens indicate that a considerable amount of fat remains at the end of hibernation. This fat disappears as spermiogenesis begins, following emergence from hibernation. A comparison of figures 3 and 6 clearly shows the inverse relationship between fat body and testicular cycles. Hahn and Tinkle (1965) found a somewhat similar fat body cycle in *Uta stansburiana*; however, their specimens did not truly hibernate during the winter and were active and feeding on warm winter days.

The spermatogenic cycles of most reptiles fall generally within one or the other of the following two categories: (1) The spermatogenic cycle and increase in testicular size is initiated in late summer or autumn and completed in spring shortly after emergence from hibernation. Maturation of sperm is more or less coincident with that of ova, and spring inseminations utilize newly produced sperm. (2) The spermatogenic cycle and increase in testicular size are initiated in spring and completed in autumn. Sperm are stored in epididymides during hibernation, and spring inseminations utilize sperm produced the previous autumn.

Most lizards studied fall within the first category. These include *Xantusia vigilis* (Miller, 1948), *Sceloporus graciosus* (Woodbury and Woodbury, 1945), *Sceloporus occidentalis* (Wilhoft and Quay, 1961), *Sceloporus olivaceus* (Blair, 1960), *Uta stansburiana* (Tinkle, 1961), *Crotaphytus collaris* (Fitch, 1956), and *Anolis carolinensis* (Fox, 1958). The cycles of some *Thamnophis* studied by Fox (1952) and a turtle, *Terrapene ornata*, studied by Legler (1960) fall within the second category.

Bostic (1966) suggested on the basis of his study of *Cnemidophorus*

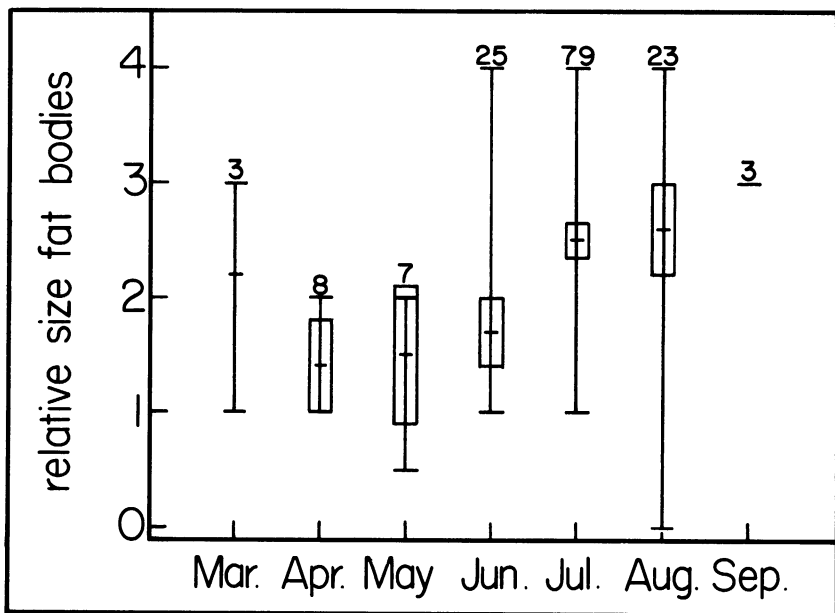


FIG. 6. Relative size of fat bodies for specimens of *Cnemidophorus inornatus* males. Numbers on the vertical axis were arbitrarily assigned with the largest numbers representing the largest fat bodies. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

*hyperythrus* that "apparently, the testes of whiptails do not increase in size just before hibernation." He found the cycle of *C. hyperythrus* to be similar to the one described for *Sceloporus orcutti* by Mayhew (1963) in which the bulk of testicular enlargement took place in the spring. Both studies indicate that sperm is not stored over winter in males. In contrast to Bostic's suggestion concerning whiptails in general, the present study has established that *C. inornatus* does begin testicular enlargement in the fall and that this enlargement continues during the winter. It also has established that no sperm is stored over winter in males of this species. In general, *C. inornatus* falls well within the first category.

The reproductive cycle of *C. inornatus* × *neomexicanus* males was discussed in Christiansen and Ladman (1968). The two cycles do not differ in the timing of any of the phases but it is unlikely that the hybrids produce enough viable sperm to effect fertilization.

#### REPRODUCTIVE CYCLE OF FEMALES

**FOLLICULAR DEVELOPMENT:** Of the 214 specimens of *C. inornatus* used

in this portion of the study, 181 were adults and 33 were juveniles. Follicular examination reported here was based only on whole, undamaged specimens. The number of individuals used in this phase of the study each month is shown in figure 1. It should be noted that only small samples are available for April and September, and data from these samples should be considered more indicative than conclusive.

Because follicular development is a continuous process at certain times of the year, it is difficult to establish criteria for defining enlarged and

TABLE 3  
PERCENTAGE OF ADULT FEMALE *Cnemidophorus inornatus* BEARING ENLARGED FOLLICLES,  
OVIDUCAL EGGS, CORPORA LUTEA, OR ATRETIC FOLLICLES  
FOR EACH ONE-MONTH PERIOD OF ACTIVITY<sup>a</sup>

Month	Total Females	Females with Enlarged Follicles		Females with Oviducal Eggs		Females with Corpora Lutea		Females with Atretic Follicles	
		No.	%	No.	%	No.	%	No.	%
May	5	3	60	0	0	0	0	0	0
June	37	24	65	6	16	11	30	5	14
July	86	16	19	3	3	14	16	21	24
August	49	0	0	0	0	0	0	2	4
September	4	0	0	0	0	0	0	0	0

<sup>a</sup>The categories for eggs and corpora lutea are not mutually exclusive.

nonenlarged follicles. For purposes of the present study, nonenlarged (i.e., quiescent) follicles of both species are defined as those less than 3.0 mm. in maximum diameter (usually much smaller) and having a translucent milky white appearance. By contrast, enlarged follicles are usually much larger (at least 3.0 mm. in diameter) and distinctly yellowish.

The reproductive cycle of females of *C. inornatus* begins in spring (see table 3) and probably in late May. None of the three specimens collected during the first two weeks of May possessed enlarged follicles, but follicles of both specimens collected during the second two weeks of May exceeded 7 mm. in diameter. Follicular development continues until ovulation at which time the follicles have an orange-yellow appearance.

The largest ovarian follicles found in this species were 8.5 to 9.4 mm. in diameter, and this is assumed to approximate size at ovulation. Many of these were characterized by a stellate arrangement of blood vessels on the follicular wall which appears to be preliminary to the onset of ovulation. The average maximum diameter of 103 enlarged follicles in *C. inornatus* was 5.6 mm.

TABLE 4

PERCENTAGE OF ADULT *Cnemidophorus neomexicanus* BEARING ENLARGED FOLLICLES, OVIDUCAL EGGS, CORPORA LUTEA, OR ATRETIC FOLLICLES FOR EACH ONE-MONTH PERIOD OF ACTIVITY<sup>a</sup>

Month	Total Females	Females with Enlarged Follicles		Females with Oviducal Eggs		Females with Corpora Lutea		Females with Atretic Follicles	
		No.	%	No.	%	No.	%	No.	%
April	7	1	14	0	0	0	0	0	0
May	31	9	29	2	6	2	6	2	6
June	46	24	52	12	28	14	30	15	33
July	75	8	11	4	5	5	7	33	44
August	44	0	0	0	0	0	0	7	16

<sup>a</sup>The categories for eggs and corpora lutea are not mutually exclusive.

Of the 271 specimens of *C. neomexicanus* considered here, 203 were adults and 68 were juveniles. The reproductive cycle of this species also begins in spring, as is indicated in table 4. A single specimen collected on April 27 possessed enlarged follicles; the remaining six specimens collected that month contained none. Follicular enlargement was evident in nearly one-third of the May specimens and more than three-fourths of the June animals containing either enlarged follicles or oviducal eggs. It appears that some individuals of *C. neomexicanus* may begin follicular enlargement two or three weeks earlier than individuals of *C. inornatus* but this cannot be said with certainty because of the small samples available.

The largest ovarian follicles found in *C. neomexicanus* ranged from 9 to 10 mm. in maximum diameter and this approximates follicular size at ovulation in this species. The average size of enlarged follicles from *C. neomexicanus* was 6.5 mm., which was nearly 1 mm. larger than the average for *C. inornatus* (see fig. 7).

It is evident from these data that ovulation of both species occurs at larger follicular sizes than the 7 mm. reported for *Uta stansburiana* by Tinkle (1961), *Xantusia vigilis* by Miller (1948), and *Sceloporus graciosus* by Woodbury and Woodbury (1945). Ovulation appears to occur at a larger follicular size among most species of *Cnemidophorus* that tend toward a larger body size than the lizards mentioned above. For example, *C. tigris* was reported by McCoy and Hoddenbach (1966) to ovulate at 11.5 to 12 mm. follicular diameter and Bostic (1966) reported ovulation at a follicular diameter in excess of 10 mm. in *C. hyperythrus*.

Females of both species in the present study were judged to have recently ovulated when large, highly vascular corpora lutea were found in the ovaries and unshelled or slightly shelled eggs were found in the oviducts.

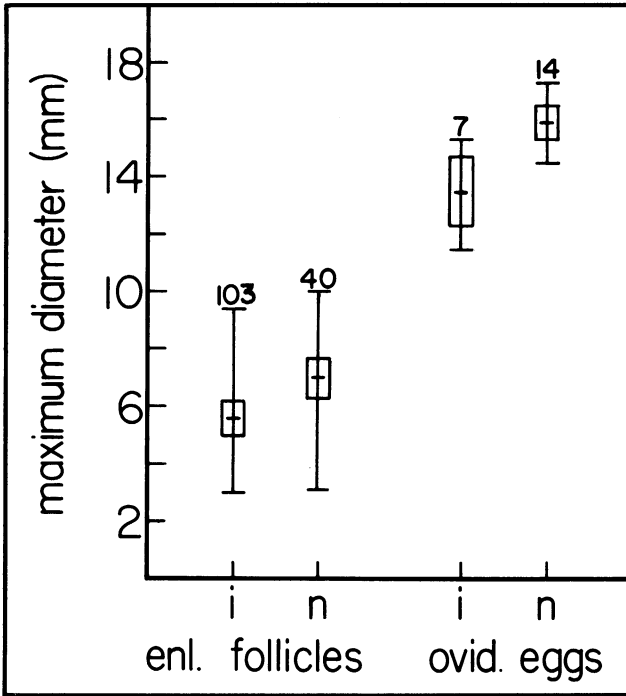


FIG. 7. Maximum diameters of enlarged ovarian follicles and oviducal eggs for specimens of *Cnemidophorus inornatus* (i) and *C. neomexicanus* (n). Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

Dates of ovulation, which were recorded on this basis, ranged from June 7 to July 12 for *C. inornatus*. Ovulations in this species for July are rare, as evidenced by oviducal eggs being found in only 3 per cent of the July specimens of *C. inornatus* (see table 3). Approximate dates of ovulation in *C. neomexicanus* ranged from May 27 to June 28. All corpora lutea for July in this species appeared old, and no estimate could be made as to when they were formed. The fact that 7 per cent of July specimens contained oviducal eggs suggests that a few individuals of *C. neomexicanus* may also ovulate during the early part of July.

Judging from the first appearance of female *C. inornatus* with enlarged follicles (May 16) and the earliest recorded date of ovulation in this species (June 7), 23 days is a reasonable estimate of the time required to attain follicular maturity. In individuals of *C. neomexicanus* the first

enlarged follicles were found on April 29 and the first ovulation was recorded on May 27 which allows 28 days for follicular development. The five-day difference between the two species could easily be the result of sampling error, and it is doubtful that the difference is significant. McCoy and Hoddenbach (1966) indicated that *C. tigris* required about 20 days for follicular development.

If the estimate of 23 days were used, females ovulating in late June or early July could represent individuals that began follicular development during the first week in June. These late-ovulating females could be older lizards producing second clutches or recently matured individuals reproducing for the first time. The fact that some lizards possessed enlarged follicles as well as corpora lutea during the first week of June is an indication that a few individuals do, in fact, lay two clutches in the same year.

The latest clearly enlarged follicles of *C. inornatus* were found in five specimens on July 4. A July 22 specimen contained a very large follicle which showed signs of atresia. The last clearly enlarged follicles in *C. neomexicanus* were found in three specimens on July 22.

**OVIDUCAL EGGS AND OVIPOSITION:** Eggs were found in the oviducts of *C. inornatus* from June 7 to July 12 and in the oviducts of *C. neomexicanus* from May 27 to July 19. In most of these specimens the eggs were well shelled, indicating that they had not been recently ovulated.

Oviducal eggs of both species are elliptical (length about twice width), smooth, and creamy white. The shells are about 0.1 to 0.2 mm. thick and have a leathery consistency. Average length of 14 oviducal eggs of *C. inornatus* was 13.5 mm. (range 11.5 to 15.3 mm.). The average for 32 eggs of *C. neomexicanus* was 15.9 mm. (range 14.5 to 17.3 mm.). This difference as shown in figure 7 would be expected because of the larger follicle size as well as the larger body size of the latter species. Eggs laid by captive females and placed on moist cotton became considerably wider than those found in the oviducts, indicating that some expansion probably occurs after oviposition due to water absorption. There was, however, no noticeable change in egg length. Changes in egg size throughout the period of incubation could not be observed because all attempts at artificial incubation of lizard eggs failed as considerable growth of mold appeared within three weeks after oviposition.

Dates of oviposition were determined by absence of oviducal eggs from expanded oviducts in addition to the presence of corpora lutea. These dates are difficult to establish because corpora lutea disappear very soon after the eggs are laid. Dates of oviposition ranged from June 7 to July 19 for *C. inornatus* and from June 3 to July 19 for *C. neomexicanus*. The most



active period of egg laying was mid-June for both species. Tables 3 and 4 show the number and percentage of females of *C. inornatus* and *C. neomexicanus* respectively that possessed corpora lutea and oviducal eggs. Neither eggs nor nesting behavior nor actual deposition of eggs was observed in the field.

The small number of specimens available in which dates of ovulation and oviposition could be determined with certainty made it difficult to determine the length of time eggs spend in the oviducts. It might be argued that the relatively small number of individuals of both species found with oviducal eggs (27) compared with the large number found with enlarged follicles (85) might indicate that the eggs spend a relatively short time in the oviducts. On the other hand, this might be related to sampling error resulting from decreased surface activity of egg-bearing females because of time spent in building the nest and in oviposition.

The first ovulation and the first oviposition of *C. inornatus* were recorded on the same day (June 7). For *C. neomexicanus* evidence of the first ovulation was found on May 27 and the first oviposition on June 3, seven days later. The more or less arbitrary figure of approximately seven days seems to be at best a minimum time for the eggs to remain in the oviducts. This would place the period during which the lizard contains oviducal eggs at about one-third the time necessary for production of enlarged follicles. McCoy and Hoddenbach (1966) indicated that the eggs of *C. tigris* remain in the oviducts for about 20 days, but these authors do not tell how they arrived at their figure. Christiansen (1965) found a period of 13 days to be the best estimate of egg retention time in *Uta stansburiana*. Tinkle (1961, 1967) and Bostic (1966) did not present this information in their published reproductive studies. Maslin (personal commun.) found that eggs of laboratory-raised *C. neomexicanus* may spend about a week in the oviducts. The length of time eggs remain in the oviducts of lizards and the necessary time of contact with the various functional parts of the oviduct would certainly be an area worthy of investigation.

Hatchlings of both species were first seen on July 19, 1966. This was 43 days after the first recorded egg-laying of *C. inornatus* and 46 days after the first recorded oviposition by *C. neomexicanus* in that year. Recently hatched individuals of *C. inornatus* (less than 33 mm. snout-vent length) and *C. neomexicanus* (less than 38 mm.) were collected as late as August 16, 1966, which was 59 days after the last oviposition recorded for the two species. An incubation period of 43 to 59 days is within the range found in most other studies of lizard reproduction. Medica (1967) found an incubation period of 42 to 62 days in *C. inornatus*, *C. neomexicanus*, and *C. exsanguis* in southern New Mexico. Milstead (1957) estimated the

incubation period of *C. tigris* and *C. inornatus* as ranging from 45 to 60 days in Trans-Pecos, Texas.

**CORPORA LUTEA:** After ovulation, the collapsed follicle becomes a corpus luteum that has the appearance of a heavy-lipped ellipsoidal saucer. No difference was observed between those of *C. inornatus* and those of *C. neomexicanus*. The corpora lutea are generally similar to those I have observed in other lizards, to those described by Tinkle (1961) for *Uta stansburiana*, and to those described much more thoroughly by Miller (1948) for *Xantusia vigilis*, a viviparous lizard.

The macroscopic appearance of corpora lutea in *C. inornatus* and *C. neomexicanus* undergoes a distinct and rapid change. Shortly after ovulation, the flabby tissue forming the collapsed follicle becomes highly vascular and has the appearance of a thick, red ring between 2.7 and 3.6 mm. in diameter. The oviducal eggs at this time are thin shelled and fragile. As the eggs gain thicker shells, the corpora lutea become orange, then yellow, and gain the appearance of thick-lipped ellipsoidal saucers. This condition is maintained until shortly after oviposition. While eggs are in the oviducts, corpora lutea range from 1.8 to 3.0 mm. maximum diameter and very little, if any, macroscopic evidence of vascularity exists. This condition was observed in most of the corpora lutea studied. At the time of oviposition, the corpora lutea are smaller (1.5 to 2.3 mm.) and tend to be lighter yellow or even cream-colored.

As mentioned earlier, virtually all specimens with oviducal eggs also had clearly visible corpora lutea. The only exception was in a single *C. neomexicanus* that was collected on June 29, 1967. Several individuals of both species possessed corpora lutea after they had laid their eggs. Corpora lutea from these specimens ranged from 1 mm. or less to about 2.3 mm. in diameter and were only slightly yellow. Because of their diminished size and lack of prominent yellow coloration, these bodies can probably properly be referred to as corpora albacantia.

The exact length of time corpora lutea remain following oviposition is not known for any lizard. That they remained visible in the lizards of the present study for at least several hours after oviposition is demonstrated by a single captive *C. neomexicanus* that laid two eggs on the morning of July 19, 1967 and possessed two clearly visible corpora lutea when examined late the same afternoon. There appears to be some indication that individual *C. inornatus* may retain its corpora lutea somewhat longer after laying its eggs than does *C. neomexicanus*. Of adult females of *C. inornatus* 16 (9%) were found with corpora lutea but no oviducal eggs, whereas this situation existed with only three (1%) of adult *C. neomexicanus*. It is likely that this difference is meaningful considering the large number

of individuals examined for each species. Further support of the hypothesis that *C. inornatus* retains its corpora lutea longer than *C. neomexicanus* is the fact that the only specimen found possessing oviducal eggs but no corpora lutea (they had already regressed) was a *C. neomexicanus*. If the life of a corpus luteum were approximately the same in the two species, it would have a longer post-oviposition life in the species which retains its eggs for a shorter period. As was indicated in the section on oviducal eggs and oviposition, *C. inornatus* may retain its eggs for a shorter period than does its parthenogenetic relative.

As yet, no specific function has been ascribed to the corpora lutea of either oviparous or ovoviviparous reptiles. In the present study large corpora lutea were seen to correlate well with the presence of oviducal eggs. In addition young corpora lutea possessed large vacuolated cells that were not found in older corpora lutea. These observations may indicate that secretions of the corpora lutea are related in some way to reptilian egg retention or to the secretory function of the oviduct. Similar assumptions were made by Miller (1948) in correlating the presence of corpora lutea with the retention of embryos in the uteri of *Xantusia vigilis*. Experiments testing this hypothesis by analysis for progesterone in corpora lutea were attempted in the present study but failed because of difficulty in refining the technique for working with the extremely small amounts of tissue available.

Within both species considered here, it is evident that in an individual clutch all ovulations occur at about the same time, that all eggs of each clutch are laid at about the same time, and that corpora lutea regress at about the same rate. These conclusions are based on the more or less uniform size and appearance of corpora lutea in any one specimen, and on the fact that corpora lutea in all instances except one corresponded to the number of oviducal eggs. In no instance was ovulation observed to be incomplete (i.e., with some unruptured, enlarged follicles and some nearly shell-less oviducal eggs). In light of these data, visible corpora lutea indicate the number of eggs laid as well as the number of follicles ovulated.

Miller (1948) and Heimlich and Heimlich (1950) studying the viviparous lizard *Xantusia vigilis*, and Saint Girons (1957) studying the viviparous snake *Vipera aspis*, all found cells of a glandular nature in corpora lutea that attained maximum development in the middle of the gestation period. They also observed that the corpora lutea began degeneration shortly before parturition. Weeks (1934), however, described the corpus luteum of *Amphibolurus* as being very short-lived and as disappearing entirely some time before the eggs are laid. It is interesting that Tinkle

(1961) found five *Uta stansburiana* with oviducal eggs but no corpora lutea. This situation might be explained either as inhibition of oviposition by some physical factor or as premature regression of the corpora lutea. If the latter were true, it, along with the evidence of Weeks (1934) on *Amphibolurus* and the single *C. neomexicanus* that had lost its corpora lutea but still retained its eggs, would serve as evidence against the corpus luteum playing a major role in egg retention in some reptiles.

**TRANS-COELOMIC MIGRATION OF OVA:** I suggest the term trans-coelomic migration of ova for the phenomenon whereby ova from one ovary traverse the coelom and come to lie in the oviduct of the opposite side. Legler (1958) referred to this phenomenon as extrauterine migration of ova, and Tinkle (1961) called it interuterine migration of ova. The latter term implies that movement of the ovum is from one uterus to another and the former term could refer to any movement of an ovum outside the uterus.

Of the nine *C. inornatus* that bore both corpora lutea and oviducal eggs, four (44%) exhibited trans-coelomic migration. In two of these specimens the movement was from the right ovary to the left oviduct and in the remaining two the movement was in the opposite direction (see table 5). Of the 17 *C. neomexicanus* that possessed both corpora lutea and oviducal eggs, nine (53%) demonstrated trans-coelomic migration. In four of these individuals the movement was from right to left, and in five it was from left to right. It should be understood that this phenomenon has been detected only when the number of oviducal eggs was unequal to the number of corpora lutea on the same side. That a reciprocal exchange of eggs may occur in reptiles has not been established by any study to date, but I believe that it has probably taken place in at least some instances.

These data imply that in both species trans-coelomic migration can be detected in approximately one-half of the clutches produced. If the undetected reciprocal trans-coelomic migration were as common, it would be possible that some eggs move to the oviduct of the opposite side in nearly all the clutches produced. In addition, there appears to be no preference of movement of ova in either direction (i.e., right ovary to left oviduct or left ovary to right oviduct). These factors indicate that the "selection of an oviduct by an ovum" might be purely a random process, ova moving to the opposite side nearly as often as to the oviduct on the same side.

Further examination of table 5 shows that, given an unequal distribution of enlarged follicles among the two ovaries, the movement of ova is not likely to be random but may result from competition for available

TABLE 5  
TRANS-COELOMIC MIGRATION OF OVA OBSERVED IN FEMALE  
*Cnemidophorus inornatus* AND *C. neomexicanus*<sup>a</sup>  
(Measurements are in Millimeters)

Species	Date	Snout-vent Length	Oviducal Eggs		Corpora Lutea	
			Right	Left	Right	Left
<i>C. inornatus</i>	June 16	56	1	1	0	2
<i>C. inornatus</i>	June 7	57	1	1	2	0
<i>C. inornatus</i>	July 4	57	1	1	0	2
<i>C. inornatus</i>	June 7	59	1	1	2	0
<i>C. neomexicanus</i>	June 3	63	1	1	2	0
<i>C. neomexicanus</i>	June 7	67	1	1	0	2
<i>C. neomexicanus</i>	June 7	68	1	1	0	2
<i>C. neomexicanus</i>	May 27	69	1	1	2	0
<i>C. neomexicanus</i>	May 25	69	2	1	1	2
<i>C. neomexicanus</i>	June 16	71	1	1	2	0
<i>C. neomexicanus</i>	June 6	72	2	1	1	2
<i>C. neomexicanus</i>	June 16	72	1	1	2	0
<i>C. neomexicanus</i>	July 22	75	2	1	1	2

<sup>a</sup>The average size of specimens showing trans-coelomic migration of ova for each species was within 1 mm. of the average size of all adult females of each species used in the present study.

space. An indication that such may be the case is that in all 10 instances in which an even number of eggs was involved, the result of the migration across the coelom was to equalize the number of eggs on each side. All these specimens involved instances in which one or the other ovary contained two ova and the opposite ovary contained none. Furthermore, the three individuals possessing three eggs showed migration of ova from the side with the ovary possessing two to the side with the ovary possessing only one, even though it still resulted in an unequal distribution of oviducal eggs. In other words, the new movement was always from the ovary with the most ova (the side with the least available space) to the side with the ovary with the fewest ova (the side initially with the most available space). In none of the 13 specimens in which this phenomenon could be observed was the reverse situation true.

Trans-coelomic migration of ova was described by Legler (1958) for *Terrapene ornata* and *Cnemidophorus sexlineatus*, by Tinkle (1959) for several turtles, by Tinkle (1961) for *Uta stansburiana*, and by Miller (1951) for *Xantusia vigilis*. Christiansen (1965) found a frequency of detectable trans-coelomic migration of only 9.4 per cent of 32 gravid *Uta stansburiana* in

northern Utah. Tinkle (1961) found a frequency of 20 per cent in the same species in Texas. Miller (1951) reported the phenomenon as occurring in 41.7 per cent of the egg-bearing *Xantusia vigilis* he studied but in no lizard has it been shown to be as frequent as the 44 per cent of *C. inornatus* or the 53 per cent of *C. neomexicanus* found in the present study.

A higher rate of trans-coelomic migration has been reported for a turtle. Legler (1958) observed a rate of 57 per cent in *Terrapene ornata*, but found that in some instances the migration resulted in unequal distribution of eggs in specimens where the ova had been equally distributed in the ovaries. Legler (1958) proposed that eggs might move to the nearer ostium until that oviduct became filled, then reflexive contraction of the full oviduct might result in the path of least resistance shifting to the other oviduct and eggs from future ovulations moving in that direction.

It would not seem necessary to resort to an explanation involving reflexive contraction of oviducts to explain the mechanism of trans-coelomic migration. As oviducal eggs tend to be posterior and lateral to the ovaries, it would seem that even if the first ovum ovulated were to have an equal chance of being deposited in either of the two oviducts, the pressure caused by the presence of that oviducal egg would force the next ovum to the oviduct of the opposite side. This would tend to equalize distribution of oviducal eggs and the same factors might force a third ovum toward the oviduct in which the egg already present had advanced the greatest distance posteriorly.

**LATE OVULATION AND MULTIPLE CLUTCHES:** It has been shown that females of several temperate reptilian species produce more than one clutch of eggs a season. Among the more notable examples in iguanid lizards are: *Uta stansburiana* (Tinkle, 1961), *Crotaphytus collaris* (Fitch, 1956), and *Sceloporus olivaceous* (Blair, 1960). Scant data exist concerning the number of clutches laid by whiptail lizards. Bostic (1966) suggested that *Cnemidophorus hyperythrus* might lay a clutch early in June and another in mid-July but he presented little evidence to support this. Fitch (1958) suggested that *Cnemidophorus sexlineatus* produces two clutches of eggs per year, one in the third week of June and another in the second week of July. He based this conclusion on disproportionate numbers of gravid females observed during those periods. Hoddenbach (1966) did not give any support for his statement that *C. sexlineatus* produces two clutches per year. McCoy and Hoddenbach (1966), in the most complete study of *Cnemidophorus* reproduction to date, found that *C. tigris* lays a single clutch per year in Colorado but two clutches, one in mid-May and one in mid-July, in Texas. On the basis of concentrations of *Cnemidophorus neo-*

*mexicanus*, *C. inornatus*, and *C. tigris* with "maturing ova, over 10 mm. long" Medica (1967) stated that there is a possibility these species may lay two separate clutches. He did not find this likely for *C. exsanguis*. Unfortunately, the possibility may exist that some of the "maturing ova" that he referred to might become atretic follicles. Considerable attention is given to this portion of the present study because detection of multiple clutches is essential in determining reproductive potential.

Many of the preceding workers who proposed two clutches of eggs per year for the lizards they studied did so on the basis of two clearly defined periods when the percentage of reproductive lizards in the population attained a peak in a given year. In the present study only one reproductive peak was attained and this occurred in the first two weeks of June when nearly 100 per cent of the adult female lizards collected possessed either corpora lutea, oviducal eggs, or enlarged follicles.

Information from the present study indicates that second clutches are possible for at least a few females of both species. A few of each species contained both corpora lutea and enlarged follicles. Three were of *C. inornatus* collected June 7, 16, and 28; two were of *C. neomexicanus* collected June 7 and 29. If we allow 23 days for follicular development and seven days for the time spent by eggs in the oviducts, the June 7 and 16 individuals of *C. inornatus* and the June 7 individuals of *C. neomexicanus* would have had time to lay their eggs by the last recorded date of oviposition (July 19). However, if the eggs spend more than seven days in the oviduct, for example the 10 days suggested for *C. tigris* by McCoy and Hoddenbach (1966), only those specimens that began producing their second clutch around June 7 would have had time to deposit it by the last recorded date of oviposition. If eggs were retained longer, possibly as long as the 17 to 21-day period suggested for the closely related tropical genus *Ameiva* by Smith (1968), even fewer specimens would lay a second clutch.

Allowing 30 days for egg production, any specimen that could have produced two clutches of eggs in a single reproductive season would have had to lay its first clutch no later than June 19 and started its second on the same date or earlier. As no individuals were found that had begun follicular enlargement while still possessing eggs from the first clutch, it follows that oviducal eggs must be laid before the next clutch begins development. It also seems likely that enlargement of the second clutch of ovarian follicles would not begin immediately after oviposition but would do so two or three days later. Making these assumptions, one can suggest that any individual that had laid its eggs prior to June 16 could successfully lay a second clutch.

Approximately 29 per cent of *C. inornatus* and 33 per cent of *C. neomexicanus* individuals possessing corpora lutea but no oviducal eggs were collected before June 16. As these figures are based on relatively small samples, especially for *C. neomexicanus*, they can only be considered rough estimates. Hence, assuming that follicular development is not impaired during the last weeks of June, the rather arbitrary figure of 31 per cent can be used as the maximum percentage of these lizard populations which can produce a second clutch in a single reproductive season in the Albuquerque area.

The high rate of follicular atresia observed in July (42% higher than any other month for *C. inornatus*; 25% higher than any other month for *C. neomexicanus*) is probable evidence that a majority of females of both species do begin to produce a second clutch but atresia begins before many of the later clutches can be ovulated (see tables 3, 4, and 5). Finally, the sparsity of specimens with oviducal eggs in July (only 3 per cent of July females of *C. inornatus* and 7 per cent of July individuals of *C. neomexicanus*) indicates that if two clutches are produced they are produced only by a relatively small number of lizards. Considering the effects of all of these factors, I will assume for purposes of calculation of reproductive potential that not more than 25 per cent of the females of each species produce a second clutch of eggs in a single reproductive season.

**FOLLICULAR ATRESIA:** Atretic follicles are characteristically granular and have a slightly wrinkled appearance. Those in an advanced state of atresia are highly vascular, somewhat flaccid, and appear more orange in color than do growing follicles. Atretic follicles can be recognized histologically by disappearance of the zona pellucida and later by appearance, in the yolk, of cells from the follicular epithelium. Atretic follicles appeared in late June, July, and early August in both species. Two individuals of *C. neomexicanus* also possessed distinctly atretic follicles in May.

Figure 8 shows that groups of atretic follicles may be larger than clutches that are ovulated and laid. When number of atretic follicles is averaged for the two years of the study, mean atretic clutch size is smaller than the mean number of enlarging follicles in the two species. This is because the data on atresia include many lizards that possessed only one atretic follicle along with two or three enlarging ones.

As no oviducal eggs were seen in either species after July 19 and no corpora lutea were seen after July 22, it seems likely that most of the enlarged follicles present during that month undergo atresia. That in July a great many follicles do indeed become atretic is indicated by the fact that at least 25 per cent more lizards of the two species possess atretic follicles in July than in any other month (see tables 6 and 7).



Considering the previously stated factors, it is possible that many late-maturing follicles become atretic at the latitude of Albuquerque, whereas such late follicles might be ovulated and fertilized at more southern latitudes where the season of growth and activity is longer. This seems especially likely in the light of the study by McCoy and Hoddenbach

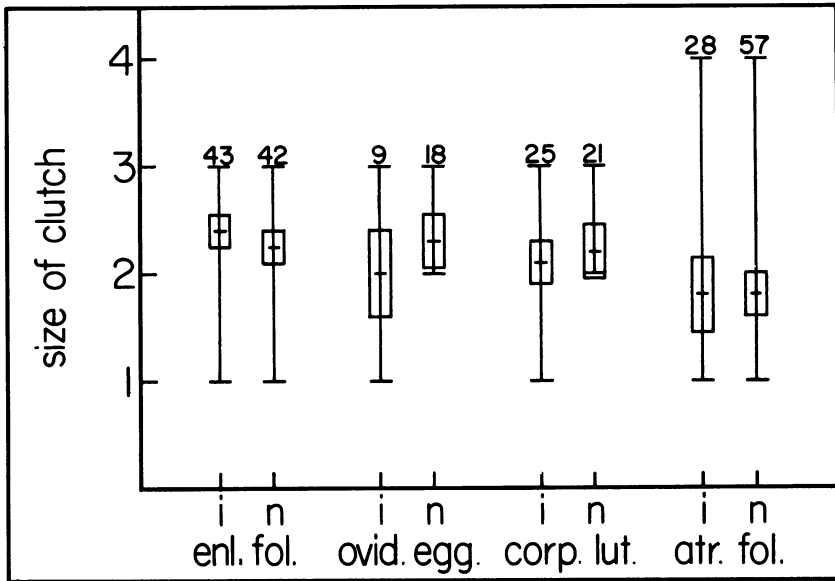


FIG. 8. Clutch size for specimens of *Cnemidophorus inornatus* (i) and *C. neomexicanus* (n) as estimated by number of enlarged ovarian follicles, oviducal eggs, corpora lutea, and atretic follicles. The latter is an estimate of size of clutches that are reabsorbed. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

(1966) in which they demonstrated that their southern (Texas) population of *C. tigris* produced one more clutch of eggs than did their northern (Colorado) population. The Albuquerque populations used in the present study are approximately midway in latitude between the two *C. tigris* populations. Considering that many *C. inornatus* and *C. neomexicanus* from Albuquerque produce a second clutch of ovarian follicles that become atretic rather than being ovulated, it is reasonable that most of the individuals in the southern New Mexico population studied by Medina (1967) produced two clutches of eggs.

**OVIDUCTS:** In order to facilitate speed of examination, a series of

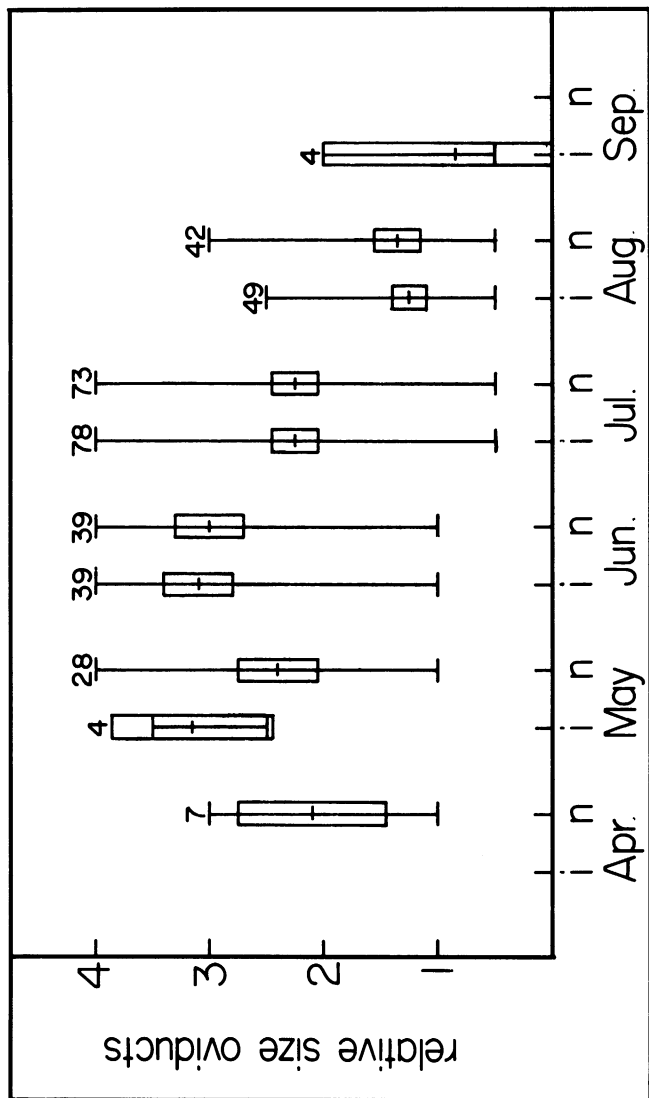


FIG. 9. Relative oviduct size in specimens of *Chemidiphonus inornatus* (i) and *C. neomexicanus* (n). Numbers on the vertical axis were arbitrarily assigned with the largest numbers representing the largest oviducts. Horizontal lines in center of rectangles indicate means; rectangles indicate 95 per cent confidence limits; vertical lines represent ranges; numerals in diagram indicate size of samples.

oviducts from each species was studied and weighed early in the course of investigation. These were divided into five weight groups for each species and numbered from zero to four respectively on the basis of increasing weight. Thereafter, oviducts were graded from zero to four on the basis of similarity to those in the original samples. The means of these figures are plotted on figure 9 and exemplify the cyclic changes in oviduct size and weight. Occasional oviducts were weighed during the course of the study to serve as additional checks for the arbitrary numbers.

It is evident from figure 9 that oviducts undergo annual cyclic changes. Oviducal weight increases to as much as 55 mg. in *Cnemidophorus inornatus* and 104 mg. in *C. neomexicanus* shortly before the ova are ovulated. The highest oviducal weights were obtained in May and June and the most notable decrease in oviducal weights occurred in July and August. The lowest oviducal weights were obtained at the end of August and in September at which time weights were as small as 5 mg. for *C. inornatus* and 8 mg. for *C. neomexicanus*.

**FAT-BODY CYCLE:** Like males of *C. inornatus*, females of that species and females of *C. neomexicanus* exhibit a cyclic change in fat-body size that varies with the gonadal cycle. The range of variation of fat-body weights of females of *C. inornatus* is not greatly different from that of the males. *Cnemidophorus neomexicanus* produces larger fat bodies, as might be expected from a larger lizard. Data were collected for the study of fat bodies of females by the same method that was used for males. The cyclic changes in fat-body mass are shown in figure 10.

Females of *Cnemidophorus* of both species contained the most fat in August and September and the least during the month of June. April and May specimens seemed to contain a little more fat than June specimens but had much less than August and September individuals. The largest fat bodies were found in a *C. neomexicanus* collected in August and the two bodies combined weighed 309 mg. The largest found in *C. inornatus* females also came from an August specimen and weighed 169 mg. June was the only month in which specimens were collected possessing no visible fat. There were two such specimens and both were *C. inornatus*. All individuals of *C. neomexicanus* that were not kept in captivity for an extended period possessed at least some fat although several individuals had less than a total of 10 mg.

These data tend to support the conclusion of Hahn and Tinkle (1965) that the greatest energy drain on lizards is not hibernation but the production of mature gametes. It should be noted, however, that the *Uta stansburiana* they studied do not truly hibernate in winter and frequently feed during this period. For this reason, their fat bodies do not

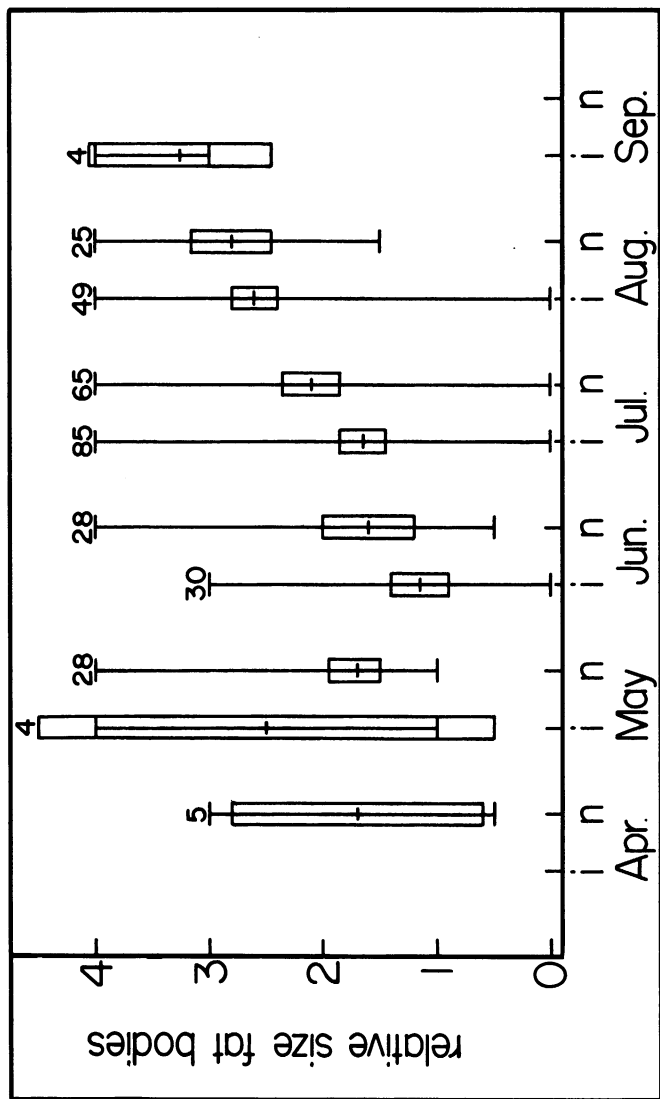


Fig. 10. Relative size of fat bodies in females of *Chemidophorus inornatus* (i) and *C. neomexicanus* (n). Numbers on the vertical axis are arbitrary with the largest numbers representing the largest fat bodies. Horizontal lines in center of rectangles indicate means; vertical lines indicate 95 per cent confidence limits; vertical lines indicate ranges; numerals in diagram indicate size of samples.

show as extreme a decrease in size and weight in winter as do the *Cnemidophorus* individuals of the present study.

Several investigators have reported indications of cyclic change in fat-body size in lizards. Among them were Hoddenbach (1966) in *Cnemidophorus sexlineatus* and Hahn and Tinkle (1965) in *Uta stansburiana*. Smith (1968) did not observe seasonal variation in fat-body size in individuals of the tropical *Ameiva quadrilineata* he studied, but he reported that females of that species that possessed enlarged follicles or oviducal eggs invariably contained smaller than average fat bodies. These works substantiate the findings of the present study indicating that oviducal growth and development of enlarged follicles utilize most of the fat remaining after hibernation and prevent the enlargement of fat bodies until the reproductive season is over. One should also consider the possibility that some of the post-reproductive season growth of fat bodies results from the freeing of follicular lipids by follicular atresia.

#### REPRODUCTIVE POTENTIAL

For purposes of the present study the term "reproductive potential" refers to the number of eggs that could be produced by an average female in an average lifetime. The number of progeny produced by one such female is considered in the text but is not implied by this term.

There are three methods of estimating reptilian reproductive potential that are based on ovarian examination rather than on nests or clutches found in the environment. Ranked in decreasing order of accuracy they are: (1) by number of corpora lutea, (2) by number of oviducal eggs, and (3) by number of enlarged ovarian follicles.

Estimates of the number of eggs per clutch based solely on enlarged follicles (method 3) are subject to some inaccuracy because some of these follicles may become atretic or may already be in the early stages of atresia and not recognized as such. In some species, but not in the *Cnemidophorus* considered here, it may be difficult to distinguish between enlarged follicles destined for the next series of ovulations and those that are not. Damage to enlarged follicles in the capture of a lizard may affect the results from this method of clutch size estimation. On the basis of several studies, including those of Legler (1960) and Tinkle (1961), one may state that ova encounter relatively few hazards between time of ovulation and oviposition. In general, the number of corpora lutea and the number of oviducal eggs (methods 1 and 2) correspond to number of eggs laid. Occasionally an individual may lay part of a clutch and retain the remainder for a short period. This happened only once during the present study and involved a captive specimen which was not provided

with nesting facilities. In freshly collected specimens, the number of oviducal eggs always corresponded to the number of corpora lutea.

For purposes of calculations of reproductive potential the number of eggs per clutch was estimated on the basis of number of corpora lutea (method 1). The mean for 25 individuals of *C. inornatus* was 2.12 eggs; the mean for 21 specimens of *C. neomexicanus* was 2.15. These averages were based only on females in which corpora lutea could clearly be distinguished and counted. As oviducal eggs were invariably found in the presence of corpora lutea, estimates based on counts of oviducal eggs involved many of the same specimens as estimates based on corpora lutea. Exceptions included 16 specimens of *C. inornatus* and three of *C. neomexicanus* which had deposited their eggs and only corpora lutea remained. The mean number of eggs per clutch based on nine *C. inornatus* specimens containing oviducal eggs was 2.0; and for 18 of *C. neomexicanus* it was 2.28. Clutch size estimates based on enlarged follicles were 2.40 for 43 *C. inornatus* individuals and 2.26 for 42 of *C. neomexicanus*. The mean number of enlarged follicles, oviducal eggs, and corpora lutea for each species is shown on figure 8. It is evident from figure 8 that no significant differences occur between the means calculated by these methods.

A tendency for females to produce more eggs per clutch as they grow larger has been reported. Blair (1960) reported this in *Sceloporus olivaceus*, and Fitch (1956) reported it for *Crotaphytus collaris*. A slight tendency for this to occur in *C. inornatus* and *C. neomexicanus* was demonstrated in the present study, but the high degree of variation of clutch size in lizards of similar body size indicated that the small differences observed might have been due to chance. Since these lizards probably continue to grow as long as they live, the question whether larger (and therefore older) females actually produce more or fewer eggs later in life is unknown.

In order to calculate reproductive potential, it is necessary to know the number of clutches laid by a single female in one reproductive season. Although no conclusive evidence exists concerning the percentage of individuals that may produce a second clutch, indications suggest that approximately one-fourth of the mature females of both species can be considered to produce a second clutch of eggs in a single reproductive season. It seems likely, in light of the high rate of follicular atresia occurring in July, that a slightly longer growing season might allow for considerably more second clutches.

Unfortunately, it was not possible in the present study to investigate life span directly, and few data are available relative to the life span of any species of *Cnemidophorus*. Milstead (1957) concluded on the basis of the very large proportion of juveniles found in the fall that most of the

adults of any given year were the young of the preceding year. He based this conclusion on a study in Texas of *C. inornatus*, *C. sacki*, *C. tessellatus*, and *C. tigris*. Contrary to this conclusion, Degenhardt (1966) found that little or no disappearance of adults or subadults occurred with the appearance of juveniles. This study was conducted with marked populations in Big Bend National Park in Texas. The observation of Milstead (1957) is more or less in line with the finding of Tinkle (1967), indicating that only a few *Uta stansburiana* live beyond their first year of adult life. On the other hand, Fitch (1958) recaptured a specimen of *Cnemidophorus sexlineatus* beginning its seventh calendar year of life and recaptured several specimens in their sixth year. Degenhardt (field notes) captured two marked adult *C. tigris* in what appeared to be their third and fourth summers of life. These data are more consistent with the findings of Fitch (1940) and Kauffeld (1948) concerning the long life span of some species of *Sceloporus*.

The large population size of *C. inornatus* and *C. neomexicanus*, combined with the small clutch size, the long period necessary for attaining maturity, and the frequent occurrence of large scarred lizards in the population, indicate that these species have long lives, possibly as long as those of *C. sexlineatus* or *C. tigris*. In the present study it might be assumed that the average adult will reproduce for at least two years, assuming that it required about two years to attain reproductive maturity, and that some, possibly 25 per cent, might reproduce a third year. It would be of considerable interest to accurately compare life span of the larger species *C. neomexicanus*, with the smaller species *C. inornatus*.

Reproductive potential for 100 females of either species hatched in August can be calculated hypothetically as follows: (1) all survive the first winter; (2) oviposition first occurs in June, approximately 22 months after hatching (i.e., in the lizards' third calendar year of life), at which time they lay 213 eggs in their first clutches and 25 individuals lay second clutches totaling 53 eggs; (3) all survive for a second reproductive season and again lay 266 eggs; (4) 25 (i.e., 25%) survive for a third reproductive season and lay a total of 66 eggs; (5) none survive for a fourth reproductive season (the fifth spring or the sixth calendar year of life). Calculated on this basis, the total number of eggs produced would be 266 at the end of the first breeding season, 532 at the end of the second, and 598 at the end of the third, if second clutches are produced by 25 per cent of the lizards each year. An average female would, therefore, produce 5.98 (approximately six) eggs in an average lifetime. If second clutches were not considered, even for a small percentage of lizards, the number of eggs produced would be considerably smaller.

If all eggs hatched, all progeny survived to breed in two reproductive seasons, and 25 per cent of them survived to breed in a third season (none living to breed in a fourth), the total progeny of 100 reproductive females would hypothetically be as follows at the end of each year.

Year	Total for year	Cumulative total
1	266.0	266.0
2	266.0	532.0
3	774.2	1306.2
4	1416.4	2722.6
5	2946.6	5669.2

The preceding figures show that approximately 5669 offspring would have been produced within the lifetime of some of the first-year hatchlings from 100 females. This compares with an estimated 787 offspring of *Uta* produced in the lifetime of the first offspring of that species (see Christiansen, 1965). These figures are based on the assumption that all eggs are successfully laid and do hatch, that all young survive, and that 25 per cent of the adults produce second clutches each year.

Neither the present study nor the literature contributes complete information on effects of the total range of predators and other hazards faced by eggs and hatchlings of *Cnemidophorus*, although several studies (Fitch, 1956; Blair, 1960; Degenhardt, 1966) discussed effects of certain predators on their populations. Unfortunately, all that can be said about these factors here is that they certainly must have considerable effect in maintaining population stability.

#### SURVIVAL ADVANTAGE

Little doubt exists today that the trend is toward progressively greater destruction and modification of natural habitats. This factor more than any other favors the expansion of *C. neomexicanus* populations and the destruction of populations of *C. inornatus*. This is likely because of the habitat preferences of the two species and probably also because of the aggressive nature of *C. neomexicanus* so that when conditions are modified such that when individuals of the two species are brought into contact the larger form may attack and drive out or kill the smaller.

The reproductive cycle of *C. neomexicanus* was nearly identical in timing and nature with that of *C. inornatus* females. Hence there appeared to be no advantage to either species in the timing of any of the factors of the life cycles. Trans-coelomic migration of ova occurred frequently in the two species, but not much more in one than in the other. The only advantages likely in the various phases of the cycle of *C. neomexicanus* may



be those associated with the lizard's larger size. This factor may provide greater protection for developing ovarian follicles and intrauterine eggs. The larger egg size may be of advantage in having greater resistance to desiccation, although I have no evidence of this. In general, it seems that if any collective advantage exists in the act of producing and laying eggs, that advantage lies with *C. neomexicanus*.

A parthenogenetic reproductive cycle may provide *C. neomexicanus* with a considerable advantage over bi-sexual forms in populating desert areas where the food supply is short. The present study established the fact that some fat is used in hibernation and much of the remaining fat is used during the time ova are being produced. Hahn and Tinkle (1965) found that females of *Uta stansburiana* from which they had removed all the fat bodies could not produce follicular enlargement, whereas sham-operated females consistently produced follicular enlargement. In areas where food is scarce, it is possible that a mating pair of lizards might not be able to accumulate enough fat to survive the winter or at least not enough to produce a normal clutch of eggs the following spring. Were a single parthenogenetic lizard to occupy previously uninhabited terrain, it would have twice the amount of food available for reproduction, and would therefore have a better chance than a mating pair of producing a normal clutch of eggs.

Clutch size in the two species is nearly identical. This is apparent whether it is estimated by counts of corpora lutea, oviducal eggs, or ovarian follicles. The amount of follicular atresia in the month of July, a critical month for second clutches, is the same for the two species and there is no evidence that a greater proportion of one species produces second clutches than does the other. Assuming that the same proportions of the species produce second clutches and that the longevity is the same, the reproductive potentials of the two species are equal when calculated on the basis of number of eggs produced by 100 average fertile females for a projected lifetime (598; 5.98 for each female). A more accurate picture of the reproductive situation of these lizards would be obtained by calculating the maximum number of eggs produced by 100 average lizards representing the normal sex ratio of the population being studied. Considering a sex ratio of 50 males to 50 females among *C. inornatus* populations, only 299 eggs would be produced by 100 lizards of this species, whereas the figure would remain 598 for *C. neomexicanus*. It is evident that this would give the latter species an advantage simply by providing the species with more individuals, each of which might have at least the same chance of survival as individuals of *C. inornatus*.

Apparently other factors, possibly also associated with the partheno-

genetic nature of *C. neomexicanus*, prevent the reproductive advantage from being as great as it might be. In a study of the sex of hatchlings and egg viability of parthenogenetic lizards, Maslin (1966) found a very low viability of eggs of *C. neomexicanus*. Only 15 of 29 clutches contained eggs that hatched and only 34 (38%) of a total of 90 eggs that were laid, hatched. Little is known about the viability of eggs of nonparthenogenetic teiids. Carpenter (1960) reported techniques for hatching eggs of *C. sexlineatus* but did not present any comparative figures on egg viability. Blair reported that only 24 (6.4%) of 376 eggs of *Sceloporus olivaceus* failed to hatch. He attributed some of these failures to drying rather than to lack of viability.

If one assumes that the eggs of *C. inornatus* are approximately as viable as those of *Sceloporus olivaceus*, the viability of *C. neomexicanus* eggs would only be 40 per cent that of *C. inornatus*. Difference in laboratory hatching techniques could easily account for a considerable difference in results, especially since the work was done by different people. Even so one might estimate that the eggs of *C. neomexicanus* are about half as viable as those of *C. inornatus*. If this estimate were correct, the difference in egg viability would compensate for the superior egg-laying ability that *C. neomexicanus* populations possess as a result of absence of males. I hypothesize that this is the major factor that prevents *C. neomexicanus* from extending its range still more rapidly.

Even though *C. neomexicanus* appears to possess several advantages over *C. inornatus*, the long-term effect of parthenogenetic reproduction is likely to be damaging. It should be expected that the genetic rigidity typical of parthenogenetic species will prevent *C. neomexicanus* from adapting to many of a variety of climatic or other environmental changes that will eventually arise.

## SUMMARY

*Cnemidophorus inornatus* and *C. neomexicanus* are teiid lizard species adapted for a dry terrestrial existence. The two species have distinct ecological preferences that favor the dissemination of one species at the expense of the other. *Cnemidophorus inornatus* is found primarily in undisturbed desert grassland but *C. neomexicanus* is found chiefly in disturbed areas, often those disturbed by man and his animals, and is able to survive under nearly metropolitan conditions.

Reproductive isolation results from the specific habitat preferences of the two species. This isolation is reinforced by an offensive attitude by the larger species *C. neomexicanus* toward the smaller species *C. inornatus*. This

was seen only once in the field but many instances were seen in the laboratory.

The two species have similar cycles of activity and hibernation. Adults cease surface activity by the third week of September, but a few juveniles remain active until the last week of September or the first week of October. Both species emerge from hibernation in mid-April. Juveniles are more active than adults during the first weeks in spring following hibernation and are also more active than adults before hibernation begins in the fall.

The reproductive cycle of the male of *C. inornatus* is initiated with the resumption of spermatogenesis in late August or September. Coincidentally, there is an increase in testicular size and weight so that immediately before hibernation these organs weigh about 9 mg., approximately three times the mean August weight. At this time they contain numerous spermatogonia and early spermatocytes. Specimens removed from hibernation in March show greater testicular weights (around 19 mg. heavier) and maximum diameters (about 2 mm. longer) indicating that testicular growth takes place during winter. This growth primarily involves production of spermatogonia and spermatocytes. Maximum testicular weights and lengths are attained in April, the first month of activity. Mean testicular weight in April is approximately 33 mg. and mean testicular length is 5.5 mm. A peak in sperm production is probably reached in May or the first week of June, probably the period of most active mating. Size and weight of testes decrease through June and July as the spermatogenic cycle is completed and the last spermatozoa mature and are eliminated from the testis. Minimum size and weight are attained in late July and early August. Mean length and weight for August testes are the smallest obtained for any month (2.5 mm. and 3 mg. respectively).

Cyclic changes in the thickness of the epididymides and vasa deferentia occur parallel to the testicular cycle. These changes appear to result primarily from changes in height of the columnar epithelium lining the lumina and produce an increase in opacity and thickness as the organs prepare to receive the spermatozoa. The fat bodies of males undergo a cycle that is approximately the reverse of that of the testes.

The reproductive cycles of females of the two species are nearly identical. These cycles begin in spring (April or May) with the enlargement of up to three ovarian follicles per lizard and follicular enlargement continues until ovulation. The first ovulations occur during the last week of May or the first week of June, therefore permitting approximately 23 days for follicular enlargement. Corpora lutea form shortly after ovulation and remain for at least a day after eggs are laid. It seems likely that these

corpora lutea have some secretory function and may be involved with egg retention. Eggs are laid from the first week of June until the third week of July, although the period of most active egg laying occurs in mid-June. Ova are retained in the oviducts for about one week. Approximately 25 per cent of the reproductive females of each species probably produce a second clutch. Many of the remaining lizards begin enlargement of follicles for a second clutch but these follicles become atretic and are never ovulated.

Trans-coelomic migration of ova is detectable in about 50 per cent of the lizards that possess oviducal eggs. It seems that this phenomenon helps to keep eggs as equally distributed as possible in the oviducts and may be of selective advantage for reasons of weight distribution.

Cyclic changes of oviducal morphology take place parallel to the phases of the ovarian cycle. These changes involve primarily hypertrophy and recession of epithelial layers surrounding the lumina and are associated with great increase in secretory activity in advance of receiving eggs. Follicular enlargement and oviduct hypertrophy correspond with decrease in fat-body size. This association may reflect the large energy drain on the organism at this time to produce oviduct hypertrophy, as well as the high demand for lipids by the enlarging follicles.

The first hatchlings appear in the last two weeks of July, and newly hatched lizards continue to be found in the population until the first week in September. The incubation period ranges from 34 to 46 days.

Mean clutch size is the same in the two species, approximately 2.13 eggs per female, but ovarian follicles and oviducal eggs are considerably larger in *C. neomexicanus* than in *C. inornatus*. It appears that approximately 25 per cent of the reproductive females of both species may lay a second clutch of eggs each year. Assuming that this is true, 266 eggs would be produced by each 100 fertile females each year. A logical estimate of longevity for a typical specimen of either species is approximately four calendar years; possibly five for 25 per cent of the specimens (individuals do not attain reproductive maturity until their third calendar year). Assuming that these estimates are correct, the mean number of eggs produced by each reproductive female would be approximately 5.98 (598 for each 100 fertile females).

Because no males exist in populations of *C. neomexicanus*, the number of eggs produced relative to the total population is approximately double that in populations of *C. inornatus*. This factor, however, may not benefit the former species directly because viability of eggs of *C. neomexicanus* may be only about half that of *C. inornatus*. The reproductive potential of the two species may therefore be effectively the same. The aggressive

behavior of *C. neomexicanus*, its preference for forms of disturbed habitat, which are becoming more and more widespread, and its ability to reproduce in areas where the food supply is too short to sustain two lizards, are probably the major factors responsible for the displacement of *C. inornatus* populations by this species.

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