THE REPRODUCTIVE CYCLE OF THE WESTERN WHIPTAIL LIZARD (*CNEMIDOPHORUS TIGRIS* BAIRD AND GIRARD) AT TUCSON, ARIZONA

by

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ABSTRACT

Males and females of Cnemidophorus tigris were collected during the active months of an entire year. Histological sections of testes and ovaries were examined. The males of Cnemidophorus tigris at Tucson, Arizona follow a seasonal reproductive cycle in which gonadal size is minimal in September-October. After emerging from hibernation in March-April, there is increase in the size of the testis, height of the seminiferous epithelium, and diameter of the seminiferous tubule. Maximum size is reached in June-July, followed by rapid regression. Ovaries undergo a period of heavy yolk deposition from early April to May and remain functional until August. One to two clutches of eggs are laid a year. A one to one ratio was noted between number of corpora lutea observed and number of oviducual eggs present. Data suggest that some of the lizards born in early August become sexually mature the following spring.

INTRODUCTION

Relatively little is known of the biology of reproduction in the bisexual teiid lizard *Cnemidophorus tigris*. Stebbins (1954) reports on copulation and egg-laying as does Milstead (1957) in a population of *Cnemidophorus tigris marmoratus* in Trans-Pecos, Texas. Recent reviews of reptilian reproduction in general may be found in Miller (1959), Dodd (1960), and Forbes (1961).

An examination of reproduction in this species, the western whiptail, was undertaken as a part of studies of reptilian reproduction initiated for species occurring in the Sonoran Desert in the vicinity of Tucson, Arizona (see Asplund and Lowe, 1964). Thus the population of *C. tigris* investigated is in the Arizona Upland section of the Sonoran Desert near the northwestern corner of the Sonoran Desert. The species has a wide distribution in western North America that is centered in desert environments and which is inclusive of bordering grasslands and woodlands.

MATERIALS AND METHODS

Adult lizards were collected at weekly intervals from June 1963 to June 1964 excluding the months of hibernation (November to February). The majority of the material was collected in Paloverde-Saguaro habitats at 2800 feet elevation in the foothills of the Santa Catalina Mountains north of Tucson, Pima County, Arizona. Most of it was concentrated in a study area of a half-mile radius near the north end of Campbell Avenue.

After the last animals of the year had disappeared in the foothills of the Santa Catalina Mountains, collections were made during a subsequent period of two weeks in October at the lower elevated Avra Valley (elev. 1950 ft.) on the west side of the Tucson Mountains, thirty miles west of Tucson (near the Trico Electric Co. Plant). These animals were collected in creosotebush habitats.

All animals were collected with dust-shot, opened and placed in Bouins fixative in the field. Testes of six animals or more a month were sectioned at ten microns and stained with Hematoxylin using the Heidenhain method. Sections were made also from June 1964 males with the use of a freeze microtome and stained with oil red O for lipids.

The diameter of the seminiferous tubules and the height of the epithelium were measured (micra) at regular intervals throughout each month. Vernier calipers were used for measuring (mm.) the snout-vent length, and, in situ, the gross testis width and the size of eggs and ovaries.

Photomicrographs were taken with a Zeiss Photomicroscope. The pictures were taken with a magnification of 400X, unless otherwise stated.

THE TESTICULAR CYCLE

Seminiferous Tubules

The testes of <u>Cnemidophorus tigris</u> as in other reptiles are elliptical white bodies suspended retroperitonealy in the body cavity. The right testis is located more anteriorly than is the left. The testis is surrounded by a tunic composed of two distinct layers. The outer is made up of six to seven layers of connective tissue. The inside layer is composed of cells closely resembling interstitial cells and contains many small blood vessels. Seasonal changes in the size and microscopic anatomy are pronounced (Fig. 1, Tables 1 and 2).

<u>Spring Emergence</u>.--From year to year the animals normally emerge from hibernation at Tucson between March 25-30 and April 10-15. At this time there is no trace of sperm in the seminiferous tubules and secondary spermatocytes are most abundant (Fig. 2). Pyramidal Sertoli cells and spermatogonia are located at the periphery of the tubules in fair numbers. Near the lumen of certain tubules, primary spermatocytes are observed to be undergoing meiotic division. A rare spermatid was observed near the lumen.

<u>April</u>.--In April, with the onset of a wave of spermiogenesis, many of the secondary spermatocytes which numerically dominated the March tubules transform into spermatids (Fig. 3). Except for sperm, spermatids remain the most abundant cells in the tubules until mid-August.

At the periphery of the tubules, spermatogonia and Sertoli cells

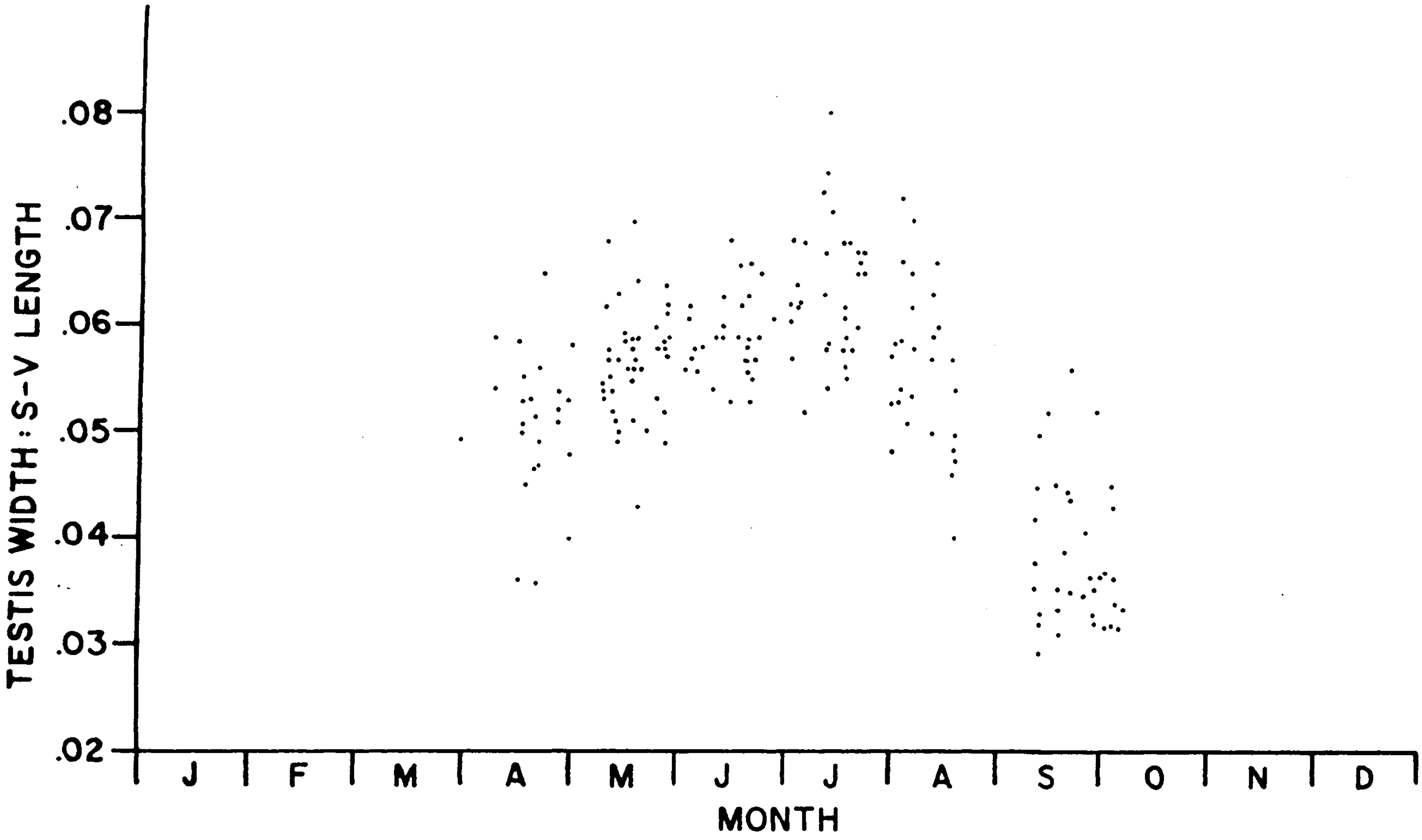

Fig. 1. Size of right testis on time for <u>Cnemidophorus</u> <u>tigris</u> at Tucson, Arizona.

Table 1. Data reductions for raw data graphed in Fig. 1. Monthly ratios of right testis width/snout-vent length in the lizard *Cnemidophorus tigris* at Tucson, Arizona.

Month	n	Snout-Vent Length (mm)		Right Testis Width (mm)		Ratio (Testis/S-V)	
		Mean	Range	Mean	Range	Mean	Range
March	1	82		4.0		.049	
April	22	74.3	(64-82)	3.8	(2.4-4.4)	.051	(.036-.059)
May	42	73.1	(63-82)	4.2	(3.3-5.5)	.057	(.049-.070)
June	27	68.7	(60-79)	4.1	(3.5-4.6)	.059	(.053-.068)
July	34	71.9	(63-80)	4.5	(3.5-3.8)	.061	(.048-.080)
August	26	72.9	(65-81)	4.2	(2.9-5.6)	.057	(.040-.072)
September	20	65.0	(61-71)	2.6	(2.0-3.7)	.040	(.029-.056)
October	12	72.6	(61-76)	2.6	(2.0-3.3)	.036	(.032-.046)

Table 2. Monthly measurements of the diameters of the seminiferous tubules and the heights of the seminiferous epithelium in the testes of the lizard *Cnemidophorus tigris* at Tucson, Arizona.

Month	Seminiferous Tubules				Seminiferous Epithelium		
	n		Smallest Dia. (u)	Largest Dia. (u)	n		Height (u)
	Animals	Tubules			Animals	Tubules	
March	1	4	12.7	30.5	1	5	17.8
April	4	16	14.7 ± .14	31.7 ± 1.6	4	20	24.5 ± .47
May	4	16	17.8 ± 1.4	31.8 ± .21	4	20	25.8 ± .80
June	4	16	18.6 ± .44	32.2 ± .18	4	20	27.0 ± .60
July	4	16	19.0 ± 1.2	32.6 ± .95	4	20	26.7 ± .05
August	4	16	12.1 ± 1.0	22.5 ± 2.0	4	20	20.1 ± 2.7
September	4	16	7.6 ± .60	15.7 ± 1.27	4	20	15.1 ± 1.5
October	4	16	6.9 ± .50	14.6 ± 1.5	4	20	11.4 ± 1.6

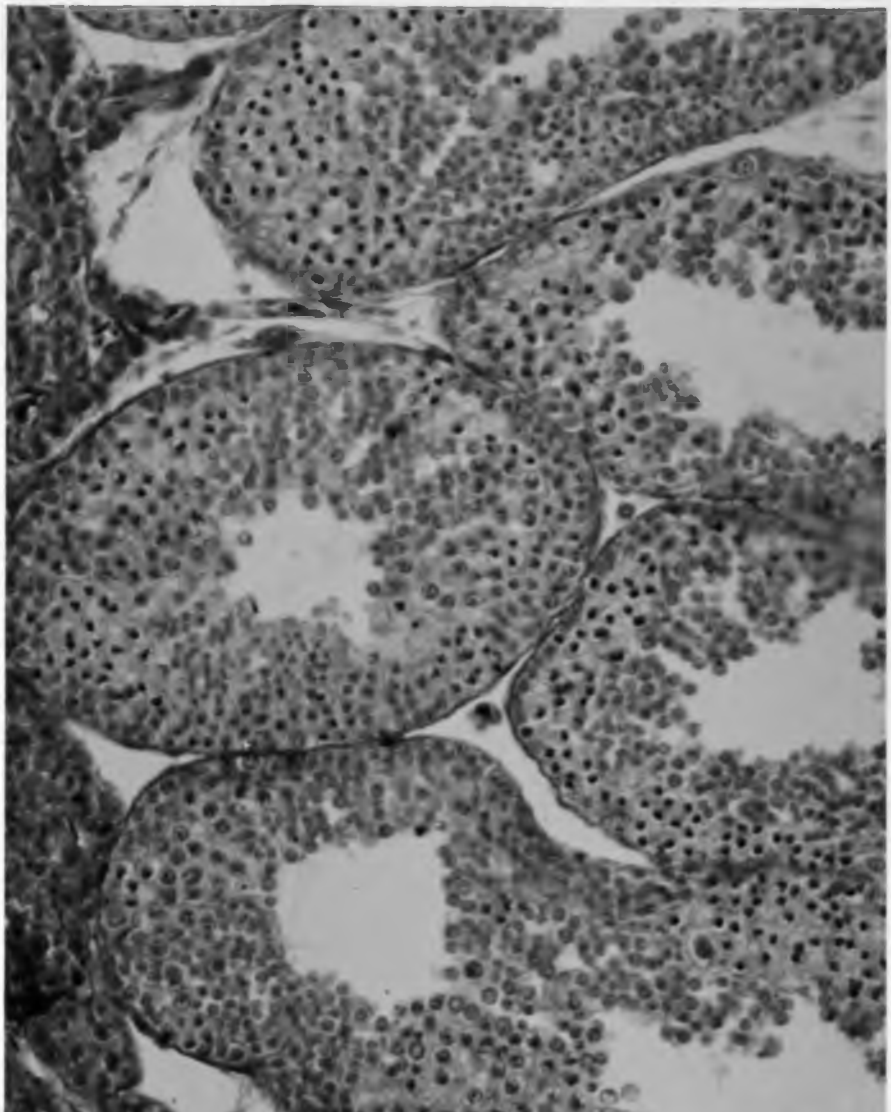

Figure 2. Late March Seminiferous tubules shortly after emergence from winter hibernation, showing abundant spermatocytes, rare spermatids and lumina. Spermatogonia and sertoli cells are seen at the periphery of the tubule.

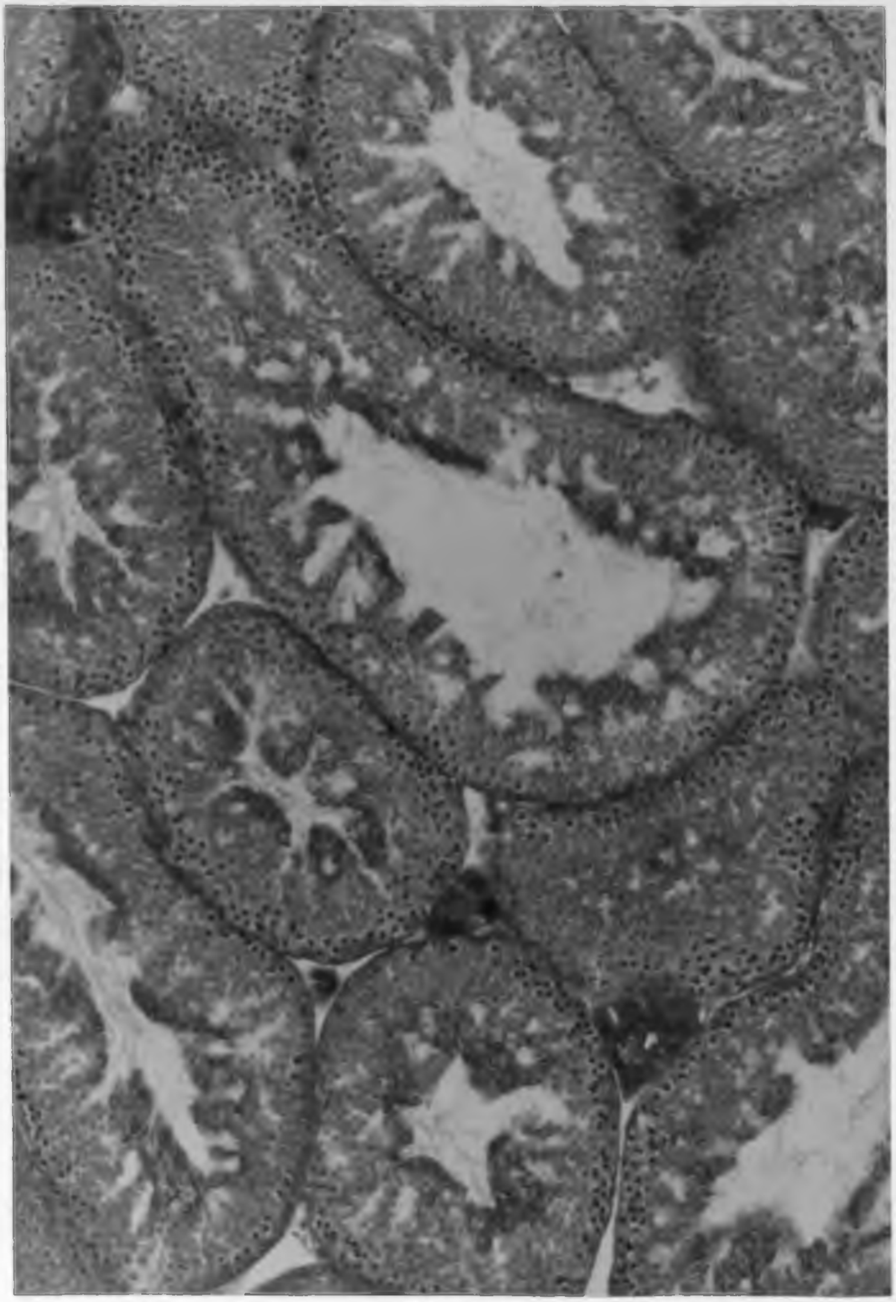

Figure 3. April 21. Seminiferous tubules with active spermiogenesis. Note clusters of interstitial cells.

are common. In many of the tubules examined, an area of primary spermatocytes three to four cell layers thick was observed to be undergoing meiotic division. Secondary spermatocytes are still seen in certain tubules but their numbers are small in comparison to their concentration in March. Six to seven layers of spermatids are located near the lumen of the tubule. Moderate quantities of sperm line the lumen and different stages in the metamorphosis of spermatid to sperm are clearly seen.

The epididymis (Fig. 4) is about fifty percent filled with sperm and the animal is capable of insemination at this time, remaining so into August.

May.--During May the process of spermiogenesis occurs at accelerated rates, with bundles of spermatozoa lying free in the lumen by the end of the month. Spermatogonia and Sertoli cells are abundant at the periphery of the tubule, and primary spermatocytes are common but their numbers are not as great as in April. A few secondary spermatocytes are seen, with spermatids being the most abundant cell.

The lumen of the epididymis is filled with densely packed sperm. Copulation was first observed in the field in mid-May.

June.--Spermiogenesis continues at an accelerated rate during June. Large and small spermatogonia are abundant at this time. Sertoli cells are common, while few primary and secondary spermatocytes are observed. Metamorphosing spermatids and sperm make up as much as ninety percent of the cells in the tubules.

In most cases the epididymis is filled with sperm: Certain animals examined possessed an empty epididymis on one side, suggesting a recent copulation.

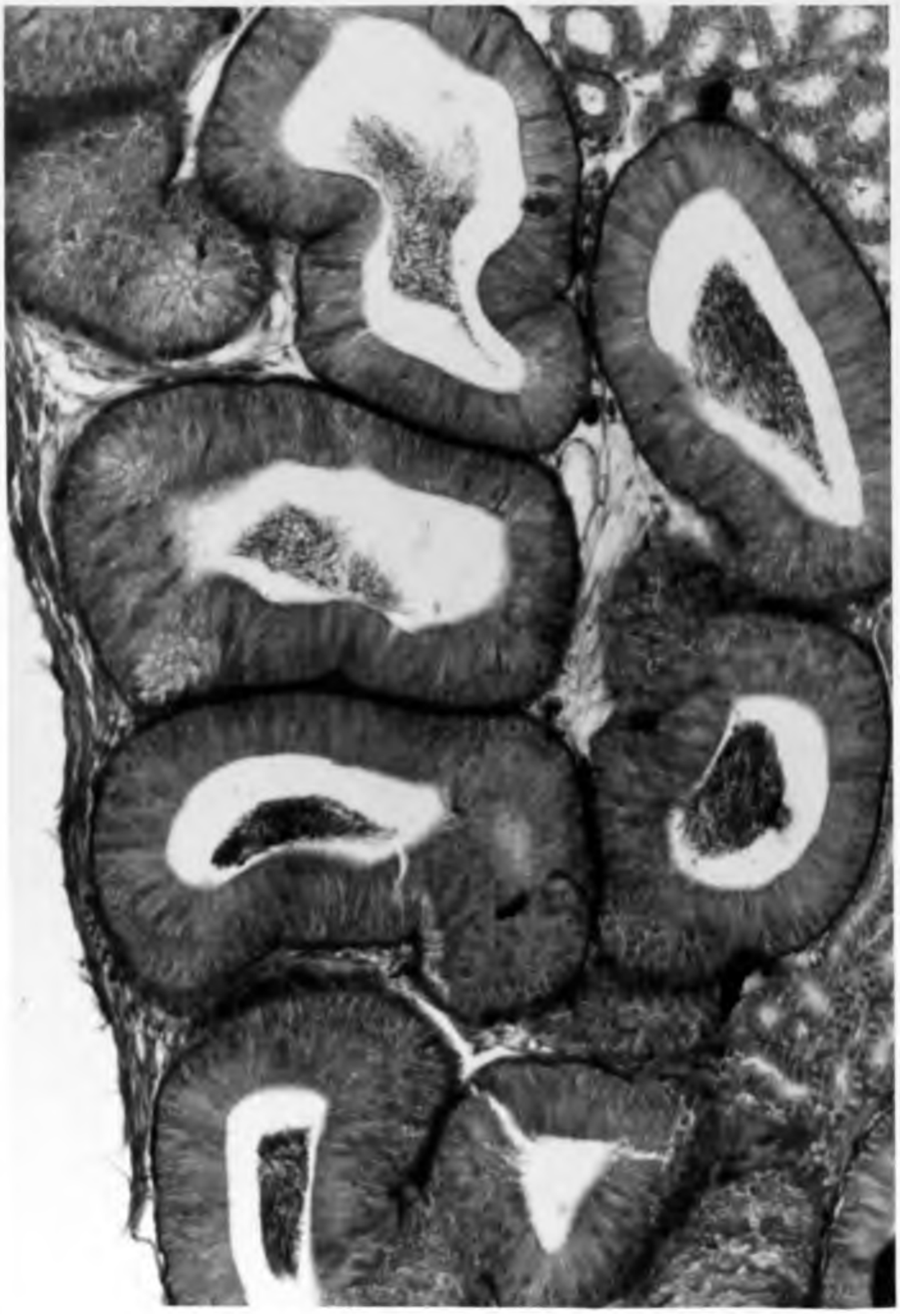

Figure 4. April 21. Epididymis partly filled with sperm.

July.--Spermiogenesis reaches peak during the last week of June into the first week of July (Fig. 5). By about mid-July the rate begins to decrease.

By late July marked individual variation in the microscopic anatomy of the testis becomes apparent. An animal examined on July 30 possessed testes which seemed to be undergoing deterioration; spaces in the tubules were filled with fibrous material, nuclei of many of the cells were pycnotic and irregular with the cellular cytoplasm being constricted, and clusters of sperm appeared to be regressing.

Throughout most of the month spermatogonia and Sertoli cells are fairly abundant at the periphery of the tubules. Isolated primary spermatocytes are occasionally seen while paired secondary spermatocytes are still common in certain areas.

The epididymides are filled with sperm throughout the month (Fig. 6).

August.--In the early part of August, most of the tubules examined were undergoing some spermatogenesis but by the latter part of the month all of the testes studied were undergoing regression. The lumina become occluded with a fibrous material and metamorphosing spermatids, which normally line the edge of the tubules are found in the center. Spermatogonia are abundant on the periphery of the tubule and primary spermatocytes are rare with secondary spermatocytes essentially totally absent.

Toward the end of the month all lumina are totally occluded by a fibrous material in which sperm heads are freely interspersed (Figs. 7 and 8). On the periphery of the tubule both large and small spermatogonia were observed. Primary spermatocytes and spermatids appeared to be

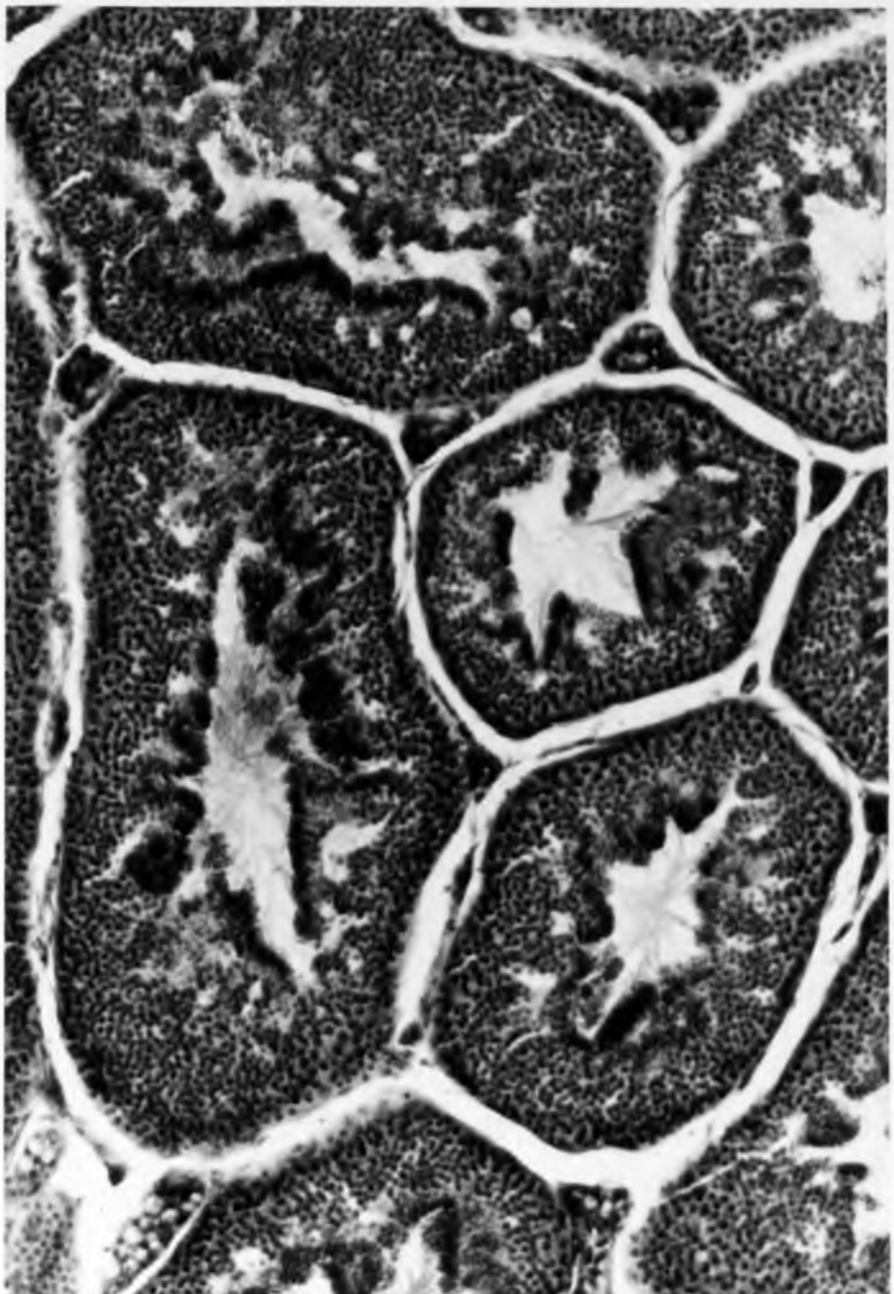

Figure 5. July 7. Seminiferous tubules; spermiogenesis is at its peak.

Figure 6. July 7. Epididymis showing densely packed sperm.

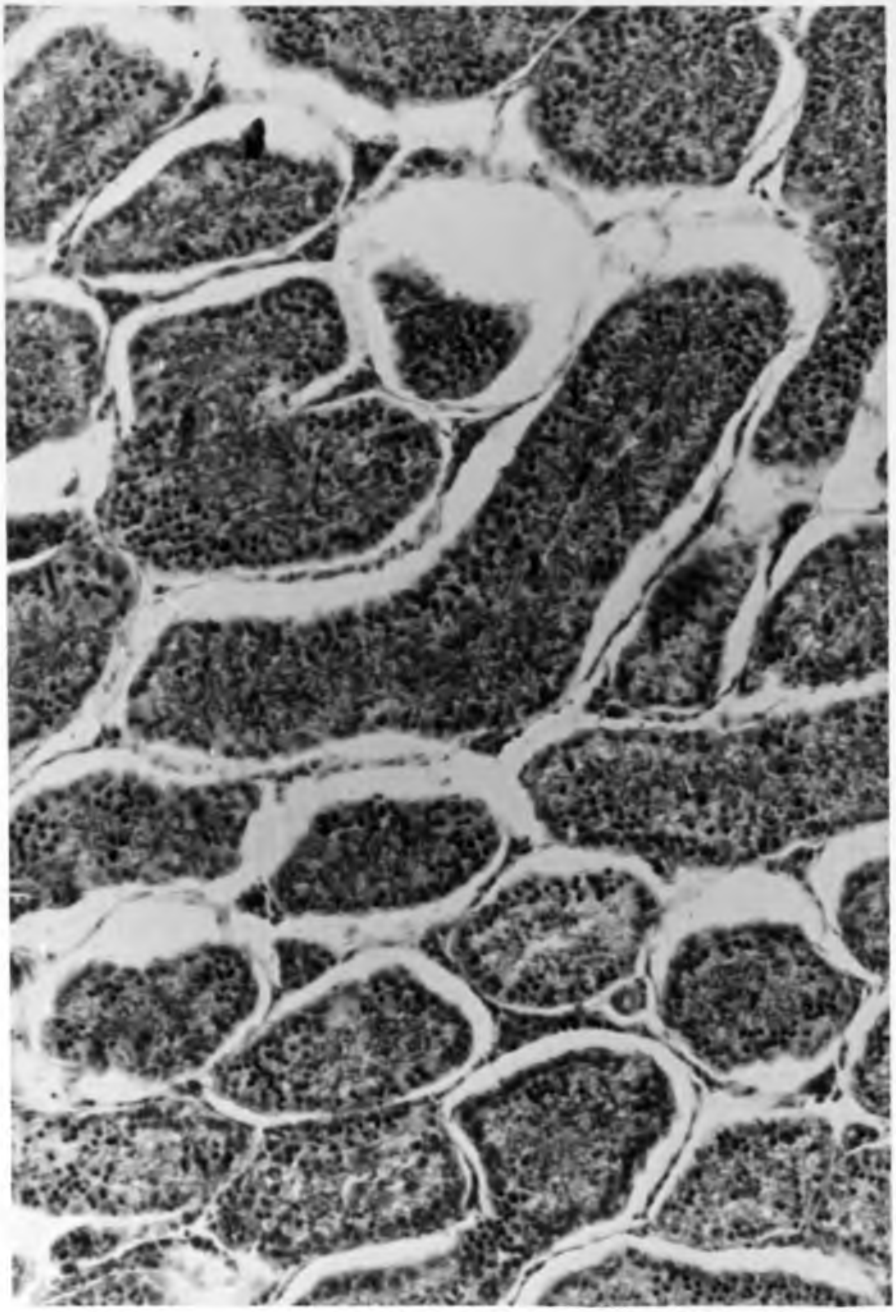

Figure 7. August 15. Seminiferous tubules; lumen has become occluded with degenerating sperm.

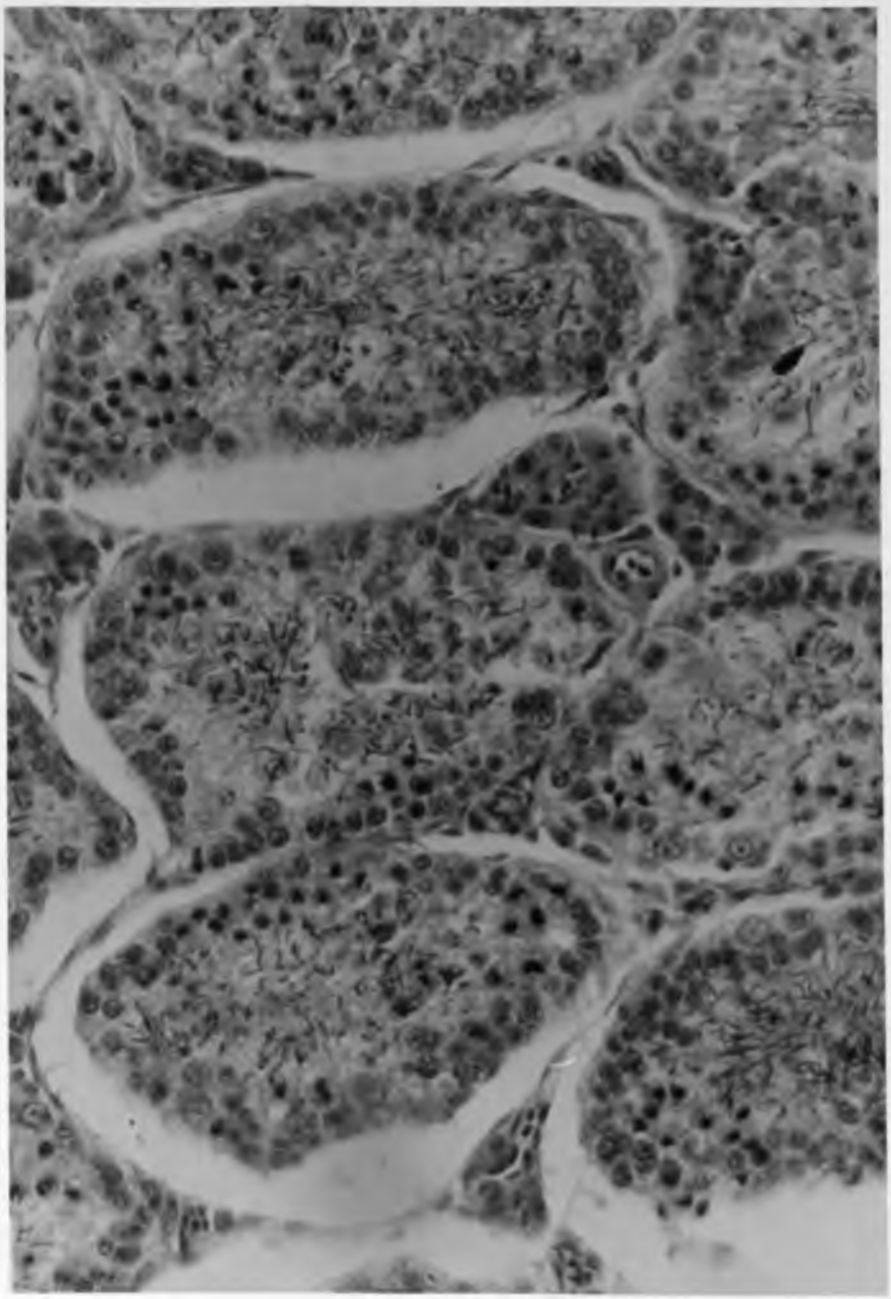

Figure 8. August 15. Seminiferous tubules showing degenerating sperm in the lumina. Heidenhains hematoxylin 900X.

degenerating at this time; the nuclei of the primary spermatocytes are highly irregular and the cytoplasm is constricted.

The epididymis of the mid-August animal is full of deteriorating sperm and cytoplasmic material among which Sertoli cells were clearly identifiable.

<u>September</u>.—By September practically all sperm are gone from the seminiferous tubules and gonadal regression is essentially complete. The tubules assume an irregular shape and the lumen remains filled with a fibrous material. Spermatogonia are abundant and are scattered throughout. This is in contrast to the March through August testis in which they are invariably found at the periphery.

Primary spermatocytes are common in certain areas and a few deeply stained secondary spermatocytes were noted. The arrangement of cells in the tubules appears to be random. In certain areas, primary spermatocytes appear to be deteriorating and their chromosomes are scattered in adjacent areas of the tubule. Sertoli cells are common and a rare spermatid was noted.

By late September most of the luminar cytoplasmic matrix including deteriorated sperm has disappeared. Certain tubules have small clear lumina which measure about 27u in diameter. Primary spermatocytes are observed to be undergoing division and are the most abundant cell in the tubules. In certain areas secondary spermatocytes are seen, spermatids being extremely rare at this time. Sertoli cells were observed on the periphery of the tubules as well as a few abortive multinucleate cells.

By the end of the month, gonadal recrudescence is apparent. Secondary spermatocytes are again the most common cell, primary spermatocytes are undergoing meiotic division and the cells are scattered randomly in the tubules.

October.--In early October the size of the lumina enlarge slightly and Sertoli cells and spermatogonia become common (Figs. 9 and 10) with continued regression of the testis. Primary spermatocytes are undergoing division and secondary spermatocytes are the most common cell. Some lumina contain a small smount of fibrous material. A few spermatids are observed, and degenerating sperm heads are scattered near the lumen. The diameters of the seminiferous tubules become smallest during this month (Table 2).

The epididymides are empty of sperm.

Sertoli Cells

When the animal emerges from hibernation in spring, Sertoli cells are fairly common on the periphery of the tubule. They remain fairly abundant as well as constant in numbers during April, May, June and July. After spermiogenesis is completed in late July their numbers decrease and at least some of them appear to be voided through the epididymides.

Because the masses of spermatozoa lining the lumina of the tubules are extremely dense, an association of spermatozoa with Sertoli cells has not been observed. At no time during spermiogenesis were these cells observed away from the periphery of the tubule. It is possible that the Sertoli cells observed in the epididymis with the deteriorating

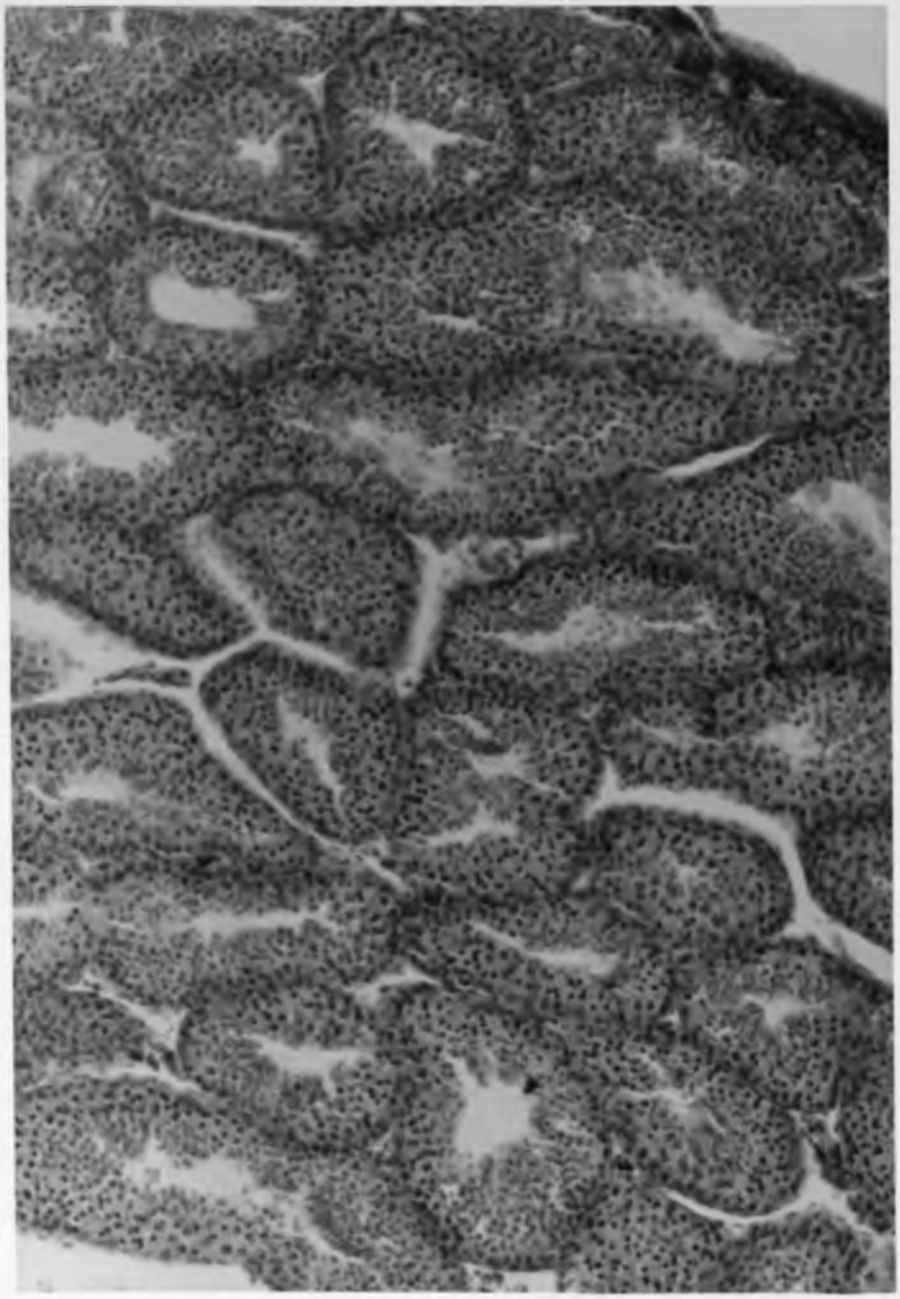

Figure 9. October 12. Seminiferous tubules showing cleared lumina.

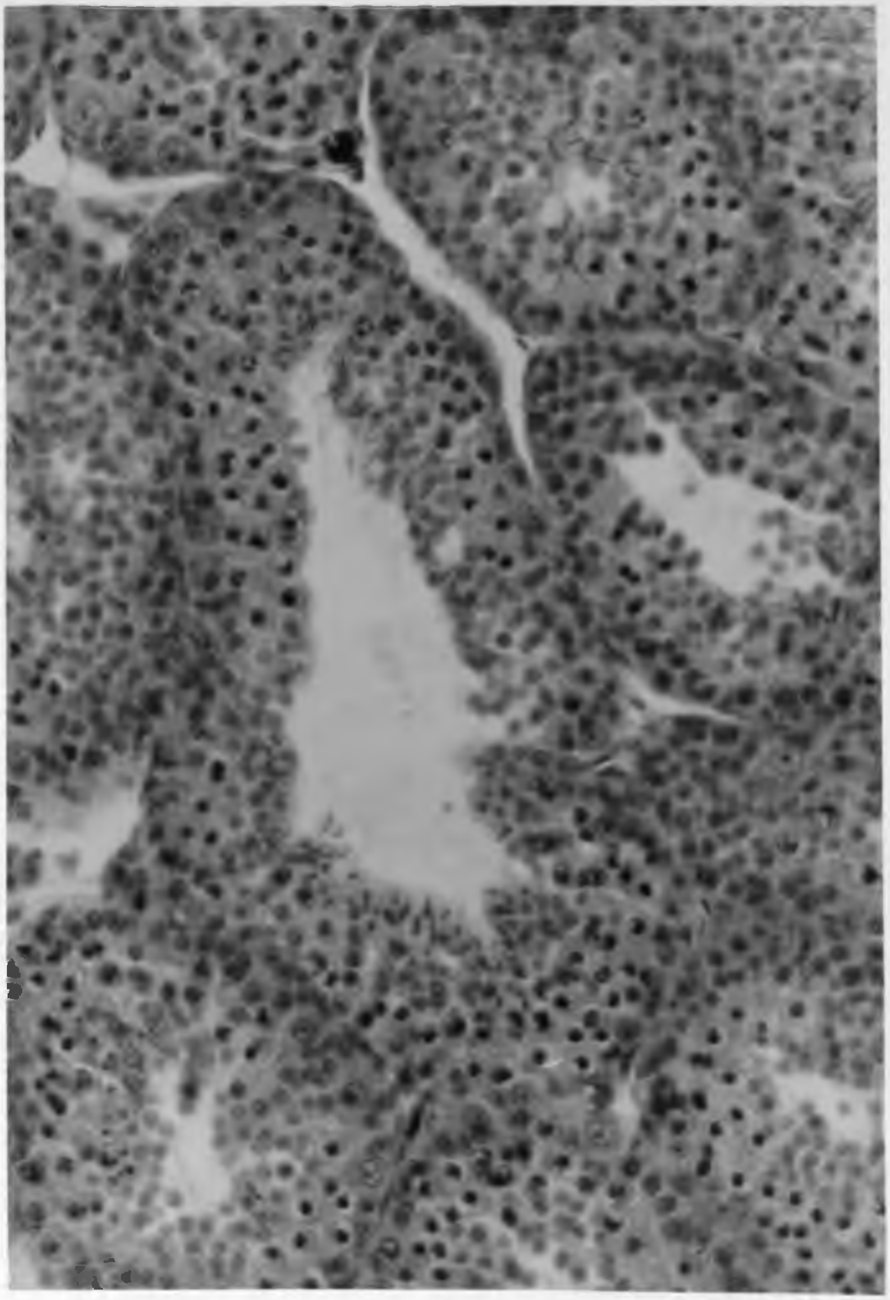

Figure 10. October 12. Seminiferous tubules; degenerating sperm line the lumina, spermatocytes are common. Heidenhains hematoxylin 900X.

sperm serve as "nurse" cells for the sperm while spermiogenesis is occurring. In August when Sertoli cells and degenerating spermatids are seen in the epididymis, other Sertoli cells were still common at the periphery of the tubule.

Interstitial Cells

The tissue between the seminiferous tubules consists of small masses of connective tissue strands with fibroblasts, blood vessels and interstitial cells. These groups of cells are fairly common throughout most of the year except in September and October when they disappear from some areas of the testis. The interstitial cells follow a cyclic pattern with the nuclei reaching maximum size from May to July.

At the time of maximum activity of the interstitial material the epididymis is packed with sperm, the hemipenis is enlarged and vasculated and the femoral pores are prominent. It is conceivable that due to their presence in large numbers during the spermatogenic cycle that the interstitial cells may serve as one of the main sources of androgens.

Three to five layers of cells closely resembling interstitial cells are found inside the tunic that surrounds the seminiferous tubules and are present throughout the year. They are cytologically similar to and slightly larger than the interstitial cells previously described. The cytoplasm is vacuolated and the area occupied by the cells is heavily vasculated suggesting a possible endocrine function. These cells which lie directly under the tunic, as well as the interstitial cells, stained pink with oil red O suggesting they may contain lipids. Moreover, because they are connected in certain peripheral areas of the tubule

(Fig. 11), there is a possibility that the interstitial cells and the cells under the tunic are functionally related.

In certain testes from September and October in which the interstitial cells have all but disappeared, the cells under the tunic are still present in large numbers. Conceivably the interstitial cells for next year's cycle originate from the tunic and pass between the seminiferous tubules where they become isolated groups of interstitial cells. A similar border of cells under the tunic was observed in another species of whiptail, Cnemidophorus burti Taylor. These cells were not found in an examination of lizards in three other families (Uta stansburiana, Callisaurus draconoides, Urosaurus ornatus, Coelonyx variegatus, Heloderma suspectum). An estimation of mean nuclear size for the interstitial cells and the cells under the tunic of the testis was obtained by measuring and averaging the longest and shortest diameter of twenty cells per animal, from four animals each month. These data are given in Table 3.

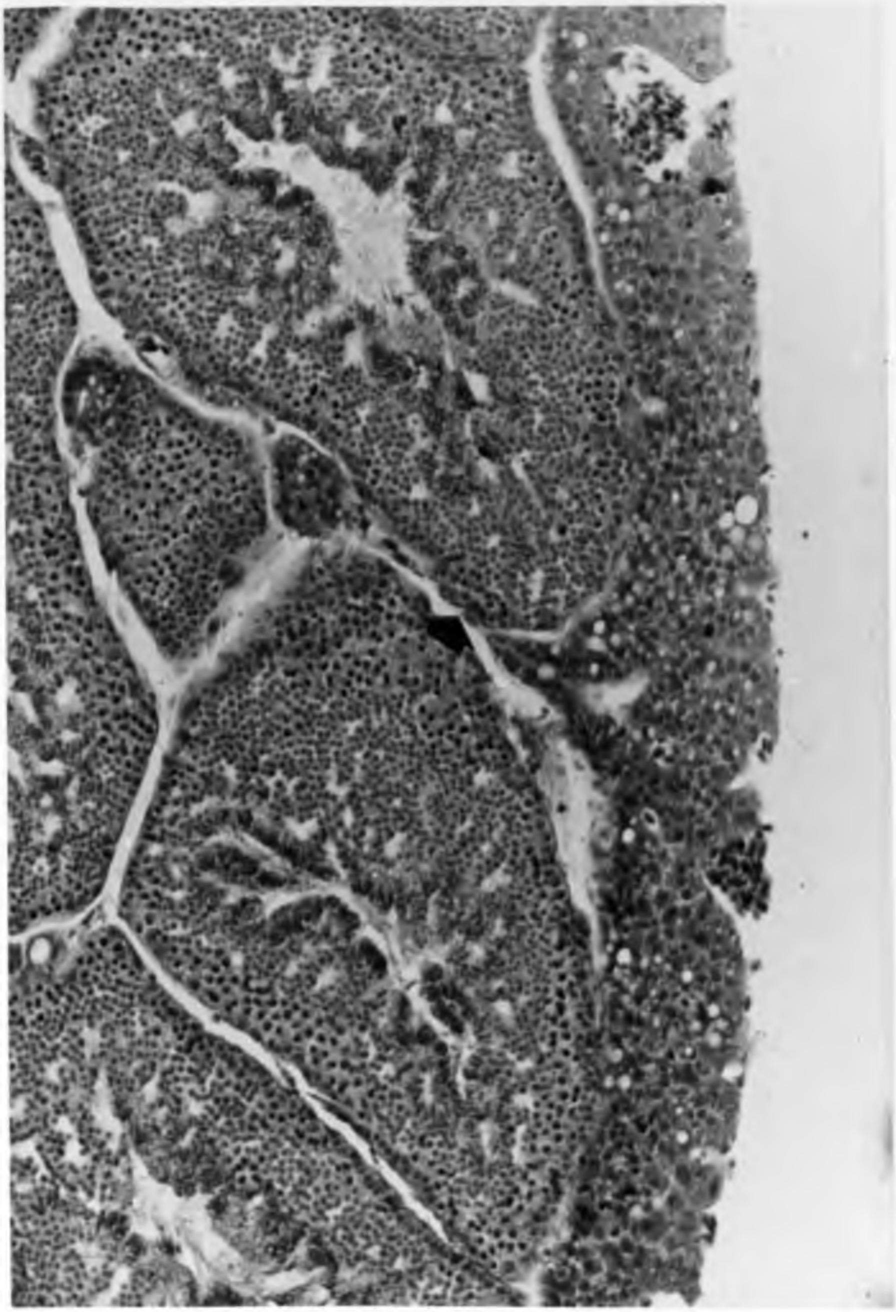

Figure 11. Seminiferous tubules from July 7, showing active spermiogenesis. At one point (arrow) the tunic cells and Sertoli cells appear to merge.

Table 3. Mean monthly diameters for interstitial cells and tunic cells of male <u>Cnemidophorus tigris</u> at Tucson, Arizona.

	Interstitial Cells (u)	Tunic Cells (u)
March	4.69	5.29
April	4.86 ± .33	5.76 ± .46
May	4.93 ± .075	5.82 ± .28
June	4.96 ± .046	5.84 ± .10
July	5.06 ± .061	5.92 ± .11
August	4.83 ± .27	5.05 ± .23
September	4.37 ± .14	4.65 ± .016
October	4.31 ± .07	4.73 ± .055

THE OVARIAN CYCLE

The oval-shaped ovary is covered by a transparent epithelium through which can be seen the ovarian elements, including developing follicles, corpora atretica, corpora lutea, germinal bed, stroma ovarii and the ovarian cavity. The germinal bed consisting of developing oogonia and oocytes is located in a small mass at the periphery of the ovary.

Ovaries and Eggs

The appearance of the follicle is similar to that described by Boyd (1941), Miller (1947) and Wilhoft (1963) for other lizards. There are four to seven follicles in the ovary during the year, their size varying with the season. On emergence from hibernation they are more or less uniform in size, with one to two enlarging during the period of yolk deposition and eventually becoming oviducual eggs. It appears that the ovulatory period is relatively short. In all females examined with two or more oviducual eggs, the conditions of the albumen and shell membranes were identical suggesting that they had been in the oviduct equal lengths of time. The most frequent number of oviducual eggs is two; occasionally three or one were noted. (A female from Hillside, Yavapai Co., Arizona, 100 miles northwest of the study area near Tucson, contained four oviducual eggs, two were in each ovary.)

Spring.--Ovaries during the month of April ranged from 2.7 mm. to 5.1 mm. (Table 4). A representative ovary contained four ova which

Table 4. Measurements of ovaries of <u>Cnemidophorus tigris</u> females at Tucson, Arizona.

	n	enlarged ova greater than 50 mm.	oviducual females	number oviducual eggs per female
April	5	0	0	0
May	14	5	3	2
June	10	3	1	2
July	15	5	2	2
August	15	5	7	2 in 6, 3 in 1
September	19	0	0	0

measured 3.2 mm., 2.9 mm., 2.3 mm., and 1.7 mm. From the middle of April to the middle of May a period of heavy yolk deposition occurs with ovulation occurring in late May. At this time the ovary contains one or two large ova, with five to six smaller ova pressed tightly against the sides of the larger.

Forty eight percent of the females examined in May contained oviducual eggs, sixty three percent contained enlarged ova with widths greater than 5.0 mm. (Table 4). Two oviducual eggs in a female (snout-vent length of 66.9 mm.) during the first week of June measured 9.2 mm. by 4.4 mm., and 10.5 mm. by 5.5 mm.

As noted earlier, copulation was first observed in the field in mid-May.

Summer.--Observations of May and June females indicate yolk deposition to be rapid. In June the number of large females encountered in the field decreases conspicuously. It is assumed that they are underground for the purpose of egg-laying. In September, after the seasonal egg-laying period (early June to late August) is over and a few weeks before retiring for the year, large females become decidedly more common on the surface.

The appearance of hatchlings ordinarily during the first week in August suggests an incubation period of about six to seven weeks. The first oviducual eggs were noted at the end of May (see above). Moreover, oviducual females were found as late as August 20 (1964). If eggs are laid on or about this date, after a six week period of incubation, the young would appear during the first days of October which are warm to hot in the Tucson area. They do appear as a rule during the first week or so of October and have two to three weeks to obtain food before entering hibernation. Enlarged ova (as distinct from oviducual eggs), noted in several females examined in late August, are probably resorbed during the gonadal regression beginning near the end of August.

Autumn.--By the end of August, egg-laying is completed for the year. Females examined in September have uniformly small ovaries, with a mean diameter of 21 mm. At this time it is difficult in many cases to distinguish ova, for the ovary has become an amorphous cylindrical mass. An ovary examined in mid-September revealed three follicles of 16 mm., 15 mm., 13 mm., and one disintegrating follicle.

By the end of September large females are gone for the year from the paloverde-saguaro foothills of the Santa Catalina mountains north of Tucson. They remain active for an additional two weeks in a warmer microenvironment in the creosotebush community of Avra Valley west of the Tucson Mountains, thirty miles west of Tucson.

Hatchlings are observed actively searching for food until mid-October in the Santa Catalina foothills, more rarely into late October--roughly one month after the last adults have been seen.

Corpora Lutea and Atreticans

A series of twelve females with oviducual eggs were sectioned during the copulation period (May-July). In all cases large secretory corpora lutea were observed, with a one to one relation between corpora lutea and number of eggs produced. The corpus luteum is an oblong body surrounded by a theca; the point at which the ripe follicle bursts becomes plugged by a mass of lutein cells (Fig. 12).

An examination of an ovary from late July, taken from an animal that had already dropped its eggs, revealed a corpus atreticans and a corpus luteum in the same ovary (Fig. 13). The corpus atreticans was triangular in shape and surrounded by a theca; fibroblasts had invaded the luteal tissue, much of which had disappeared, and large vacuoles were present throughout the cytoplasm (Fig. 14). The corpus luteum was starting to undergo degenerative changes; secretion is presumably diminished at this stage. The presence of a corpus atreticans and a corpus luteum in the same ovary suggests that this female had two broods of young--the corpus atreticans from a spring brood and the corpus luteum from a summer brood.

Figure 12. Portion of corpus luteum (arrow) from June ovary. Spot at which ovulation occurred has become plugged with luteal cells.

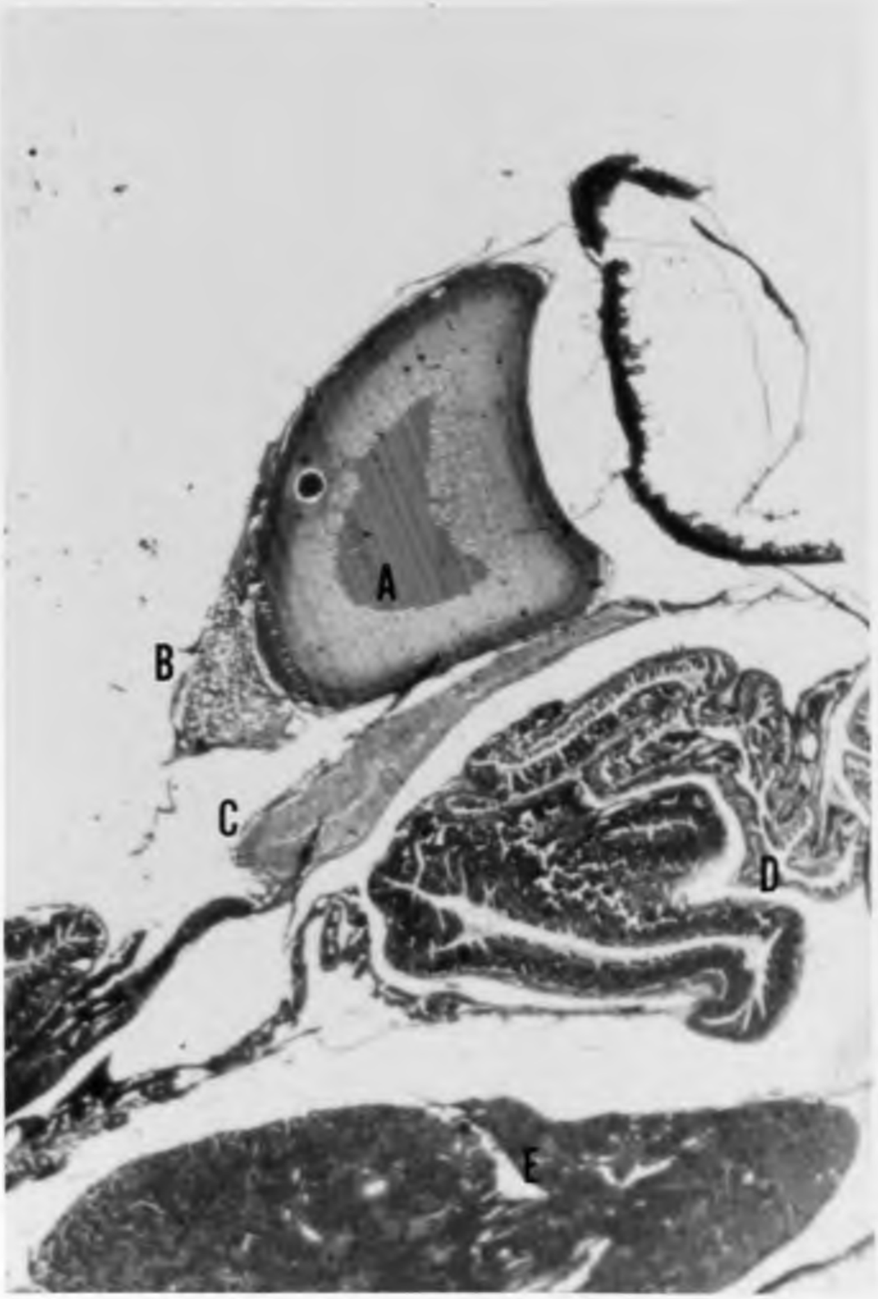

Figure 13. Corpus luteum and corpus atreticans in same July ovary (see text), follicle (A), corpus atreticans (B), corpus luteum (C), oviduct (D), and kidney (E).

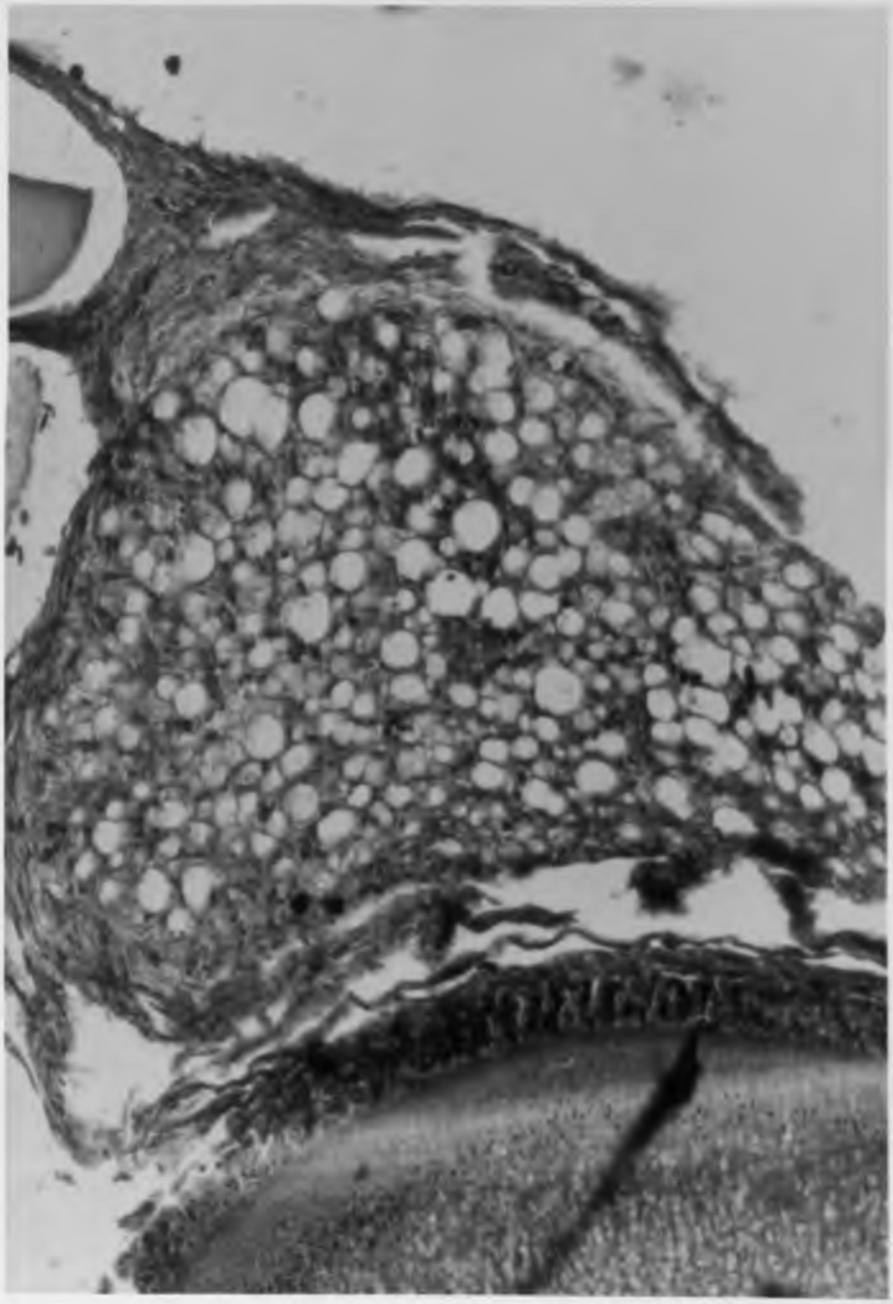

Figure 14. Corpus atreticans from July ovary.

DISCUSSION

As noted, copulation occurs during the period May-July. Within this time there appears to be two definite mating peaks. The first occurs in May, the second in July. The diurnal July activity, in contrast to the mid-day spring activity, is familiarly bimodal with the early morning (7:00 A.M. to 9:00 A.M.) and late afternoon (4:30 P.M. to 6:00 P.M.) periods of surface activity separated by an inactive period.

One or two clutches of eggs are laid each year. Milstead (1957) reports one brood per year for the subspecies Cnemidophorus tigris marmoratus in Trans-Pecos, Texas. Two clutches are facilitated by a long breeding season (May-July), ample opportunity for repeated matings, and the rapid rate of yolk deposition permitting egg-laying in early June and again in late August.

It is suggested that some of the animals born in early August are capable of reproducing the next year. For example, a female collected September 1, 1964, with a snout-vent length of 58 mm., had a brightness of the dorsal color pattern and a blue tail (which fade in older animals) which are clear indications that the animal was born that summer. When one considers that such a lizard has as long as seven to eight more weeks to feed before entering hibernation, and that females collected the following mid-May have snout-vent lengths of as short as 60-62 mm. and contain oviducual eggs, it is beyond reasonable doubt that the animals collected in September with snout-vents as long as 57-59 mm. are freely capable of reproducing the next spring.

Similarly, it is likely that some of the males born in early summer are capable of reproducing the following year. The testes of males collected in June with snout-vent lengths of 59-60 mm. were found to be undergoing spermatogenesis. A young male collected September 28, 1964, with a snout-vent length of 57 mm., possessed a blue tail and a dorsal color pattern which strongly suggested that it was born during that previous summer (ca. 2 months earlier). It appears certain that by the following spring, this animal could have reached the size of the two reproductively mature animals noted above for June (59-60 mm.).

Due to unusually cool temperatures in the spring of 1964, the whiptail lizards were 4-5 weeks later than usual in emerging from hibernation in the Tucson area. The spermatogenic cycle, however, did not appear affected by this delay in appearance at the ground surface. The testes of animals emerging from winter hibernation in late March normally have no traces of sperm, few spermatids and secondary spermatocytes as the most common cell (Fig. 1). In contrast to this situation spermatogenesis was already occurring in the testes of the first adults to emerge May 11 at Tucson, and breeding activity was observed the following day. A comparison of the testicular histology of June 1963 and June 1964 animals showed them to be identical in pertinent aspects.

SUMMARY AND CONCLUSIONS

Reproduction in *Cnemidophorus tigris* at Tucson, Arizona follows a seasonal cycle in which gonadal size is minimal in September-October. Male reproductive organs gradually recrudesce during the winter months. After emerging from hibernation in March-April the testis, seminiferous epithelial height and tubule diameter gradually increase in size through April and May, reaching maximum size in June-July followed by a rapid regression in August.

Mating is first observed in the field in May.

The ovaries undergo a period of heavy yolk deposition from early April to May, and remain functional until August. Females lay either one or two clutches of eggs a year, with one to three eggs per clutch, the usual number being two (2.2). A one to one ratio was noted between number of corpora lutea observed and number of oviducual eggs present.

The data suggest that some of the hatchlings born in early August at Tucson become sexually mature the following spring.

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