

Endocrine Function and Reproductive Impairment in an Irradiated Population of the Lizard *Uta stansburiana*

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This study describes gonadal changes in lizards (*Uta stansburiana*) exposed to chronic low levels of γ radiation (1.5-10 R/day) under field conditions and attempts to evaluate endocrine involvement in these changes. Reproductive impairment in irradiated males is demonstrated during the breeding season by reduced testes weights and by seminiferous tubules devoid of germ cells. Ultrastructural morphology of Leydig cells, plasma testosterone levels, and developed accessory sex structures indicate normal steroidogenesis in such males; cytology of the pituitary gonadotropes and pituitary gonadotropin content indicate normal gonadotropin levels. These findings suggest that low levels of radiation affect the spermatogenic process directly, rather than through damage to the pituitary. Comparable irradiation causes complete resorption of ovarian tissue in some female *Uta*. The oviducts are atrophic and the pituitary gonadotropes hyperactive. Resemblance of gonadotropes to those of castrated animals and reduced pituitary hormone content suggest elevated levels of gonadotropin production, probably due to the absence of ovarian steroid feedback in affected animals. The continued mitotic activity of oogonia in adult reptiles and their limited number contribute to the vulnerability of germinal tissue in irradiated female lizards. Destruction of the germ cells is accompanied by resorption of all ovarian tissue including steroidogenic elements. Thus, in females as in males, radiation appears to damage gametogenesis rather than pituitary function.

INTRODUCTION

Chronic exposure to γ radiation at doses as low as 2 to 10 R per day has been found to cause virtually complete loss of ovarian tissue in free-living lizards of several species, e.g., *Phrynosoma platyrhinos* (1), *Crotaphytus wislizenii* and *Cnemidophorus tigris* (2), and *Uta stansburiana* (3, 4). Except for a single male *Crotaphytus wislizenii* showing evidence of spermatogenic impairment, previous observations indicated that these radiation effects were confined primarily to females (2). Thus far, there is little information on the physiological basis of

reproductive impairment in irradiated lizards, although the failure of sterile females to respond to exogenous gonadotropins suggested that sterility was not due simply to hormone deficiency (2).

The present report has two objectives. First, we suggest that reproductive impairment in irradiated male *Uta stansburiana* is more widespread than previously recognized, and we document the effects of irradiation on testicular function in this lizard. Second, we evaluate pituitary function in relation to radiation-induced reproductive impairment in both sexes. This was done by examination of adenohipophysial and gonadal cytology and by measurements of pituitary gonadotropin content and of plasma androgen and thyroxine (T_4) titers. Accessory sexual structures, thyroids, and adrenal glands were also evaluated histologically.

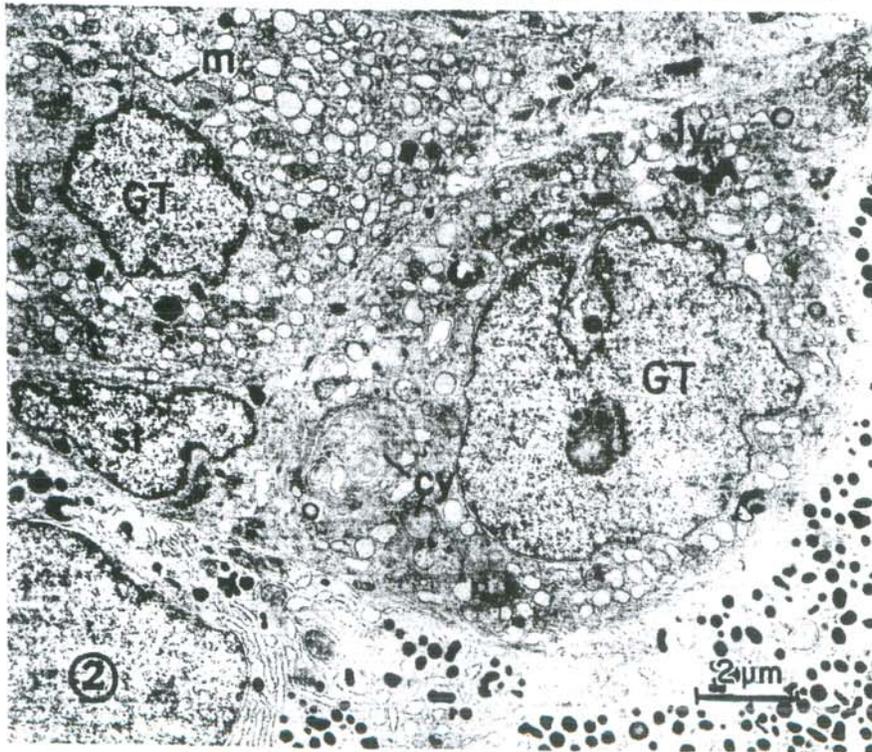
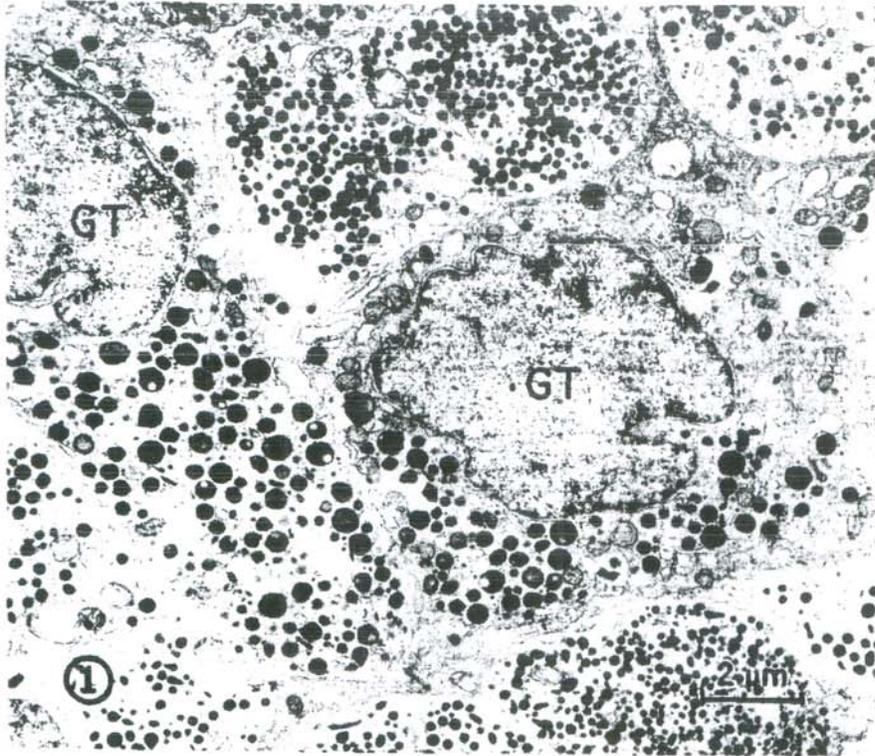
MATERIALS AND METHODS

Collection of Animals

Uta stansburiana is a 3- to 4-g, ground-dwelling lizard common in the deserts of the southwest. The 84 lizards (37 irradiated and 47 control) examined in this study were adults of several age classes collected between July 1975 and June 1977 in Rock Valley, Nevada Test Site, Nye County, Nevada. The irradiated animals occupied a circular, fenced area of about 9 hectares containing natural desert vegetation. Since 1964, this enclosure has been continuously subjected to low-level γ radiation from a centrally located ^{137}Cs source. Exposure rates within the enclosure vary between 1.5 and 10 R/day, depending on the decay of the source and the particular site within the enclosure. Control lizards were obtained from radiation-free areas nearby. These same populations of *Uta* have been the subjects of extensive demographic studies, and much is known of the natural history of the species (5-7). Both males and females breed at slightly less than 1 year of age, and females usually lay three to five clutches of eggs (three or four eggs per clutch) between mid-April and early July. Animals in their first year generally make up to 70 to 83% of spring populations and lay up to 79% of all eggs (7). Since radiation-induced resorption of one or both ovaries occurs only in females over 11 months of age (4), the irradiated population has been able to maintain apparently normal densities and age distributions (3).

Tissue Fixation and Cytology

Lizards were killed by decapitation, and selected tissues were dissected out promptly and fixed by immersion. The most satisfactory fixative was 1.6% glutaraldehyde and 0.3% paraformaldehyde in 0.8 M sodium cacodylate buffer at pH 7.4. One series of testes and kidneys was embedded in glycol methacrylate for light microscopy. The majority of tissues, however, were postfixed in 2% osmium tetroxide in 0.8 M sodium cacodylate buffer, dehydrated in ethanol, and embedded in Spurr's epoxy resin. Sections, 0.5 to 2.0 μm thick, were made of all tissues and were stained with a polychrome stain utilizing methylene blue, azure II, and basic fuchsin. Ultrathin sections were stained with ethanolic



uranyl acetate and Reynold's lead citrate and were examined with either a Zeiss 9S or a Siemen 1A electron microscope.

Since the pituitary-gonadal axis is central to our investigation, it was essential to identify the gonadotropin-producing cell (gonadotropes) in *Uta*. Castration typically results in unusually active gonadotropes, due to their negative feedback control by gonadal steroids, and this manipulation is commonly used in the identification of gonadotropes (8, 9). For this purpose, four freshly captured, nonirradiated male *Uta* were castrated in January, a time of active spermatogenesis (and presumably active gonadotropin production). The castrated lizards were maintained with controls at 32°C and long (15-hr) photoperiod for 14 days. Pituitaries were then fixed as outlined above for electron microscopy and the secretory cells in the castrated *Uta* were compared to those of four initial and four experimental controls.

Hormone Assays

Pituitary gonadotropin content was assessed by competitive binding assays employing gonadal receptors prepared from testes of the lizard *Anolis carolinensis* and ¹²⁵I-labeled human follicle-stimulating hormone (hFSH) as tracer, as described earlier (10). Pituitaries to be used for this purpose were removed from freshly killed animals and homogenized in buffer. Because their small size precluded accurate determination of pituitary weights, gonadotropin content is expressed per pituitary.

Plasma testosterone levels were determined by radioimmunoassay as described previously (11), and radioimmunoassay was also used to determine plasma thyroxine content.

All statistical comparisons were made using the nonparametric Mann-Whitney *U* test; values of $p > 0.05$ were considered not significant.

RESULTS

Identity of Gonadotropes

More than 30 *Uta* pituitaries were examined at both light and electron microscope levels. Several types of secretory cells can be distinguished, some of which are restricted in their distribution within the pars distalis (PD). The cells most conspicuously affected by castration occur throughout the PD and also in the juxta-PD part of the pars tuberalis tissue. In all control lizards in January these gonadotropes have round secretion granules ranging in diameter from 100 to 600 nm and of various electron densities (Fig. 1). Scattered cisternae of granular endoplasmic reticulum and the presence of Golgi areas suggest synthetic activity. In the anterior PD, such cells occur among two other types of secretory cells which are more restricted in their distribution to the rostral part of the gland.

FIG. 1. Gonadotropes (GT) in the anterior pars distalis of a control male *Uta* in January. Many round secretion granules of various sizes and densities are in the cytoplasm.

FIG. 2. Comparable micrograph from a male lizard 14 days after castration in January. The gonadotropes (GT) are degranulated and contain ribosome-lined vesicles, lysosomes (ly), and cytosegasomes (cy). Mitochondria (m), stellate cell nucleus (st).



FIG. 3. Active gonadotropes (GT) of control male in the breeding season (April). The cells are polarized, with secretion granules at one end and vesicles of granular endoplasmic reticulum (ves) at the other. A dark body (db) is seen on the maturing face of a Golgi stack (inset).

In castrated lizards, these latter two cells remain recognizable, while the presumptive gonadotropes are degranulated, and the cytoplasm is filled with rounded vesicles of granular endoplasmic reticulum (Fig. 2). Numerous cell sections have profiles of long Golgi stacks; the presence of many enlarged mitochondria, lysosomes, and cytosegasomes also reflect heightened activity (Fig. 2). General cytological features as well as the distribution of the implicated granulated cell in the PD of *Uta* are similar to the gonadotrope of other lizards (8, 9).

Irradiation Effects: Males

Comparisons were made of the ultrastructure of gonadotropes in irradiated and control males in April and in June. In neither month could morphological

characteristics be found to distinguish between gonadotropes of the two groups. In April these cells appear to be actively synthesizing hormone. Longitudinal cell sections reveal many round secretion granules in the vascular poles of the cells, somewhat separated from the synthetic organelles in the stellate-follicular pole by the nuclei with their large nucleoli (Fig. 3). In the synthetic area are located cisternae of granular endoplasmic reticulum, mitochondria, occasional lysosomes including lipid bodies, and many elongated stacks of Golgi saccules with numerous accompanying Golgi vesicles. Myelin bodies can be found on the periphery of these active cells, and there are also small dark bodies which sometimes occur within the cisternae but can also be seen in Golgi saccules (Fig. 3).

In June, the gonadotropes of males frequently have areas with many secretion granules at the vascular poles of the cells and expanded cisternae of granular endoplasmic reticulum at the opposite poles. The Golgi areas, however, are infrequent, reduced in size, and with few accompanying vesicles. The dark bodies seen in gonadotropes in April are not present.

Testis weights of control *Uta* generally exceed those of irradiated animals throughout the breeding season (Fig. 4). Testes from April, May, and June samples of the two groups were compared histologically. In all controls the testis tubules contain germ cells in all spermatogenic stages, and abundant sperm occur both in the tubules and in the epididymides (Fig. 5). Testes of irradiated males in these spring samples frequently had a grossly visible mottled appearance. Histological sections show that the mottling is caused by marked differences in the spermatogenic activity of the tubules: Some testis tubules have a full complement of spermatogenic stages, while other tubules in the same testis are lined by only Sertoli cells (Fig. 6). In April and May, five of eight irradiated males

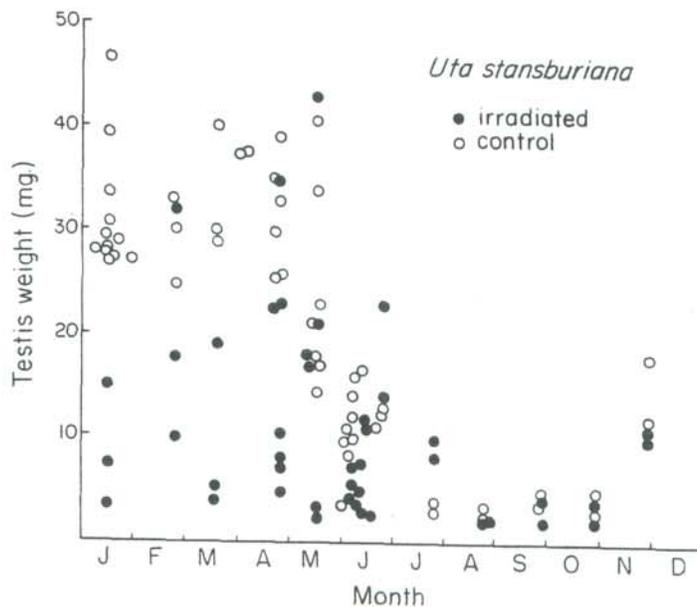


FIG. 4. Weights of one testis of control and irradiated *Uta* throughout the year. Weights from animals used in our investigation are supplemented by data on 26 irradiated and 26 control lizards collected between October of 1972 and September of 1973. All lizards were 8 months of age or older.

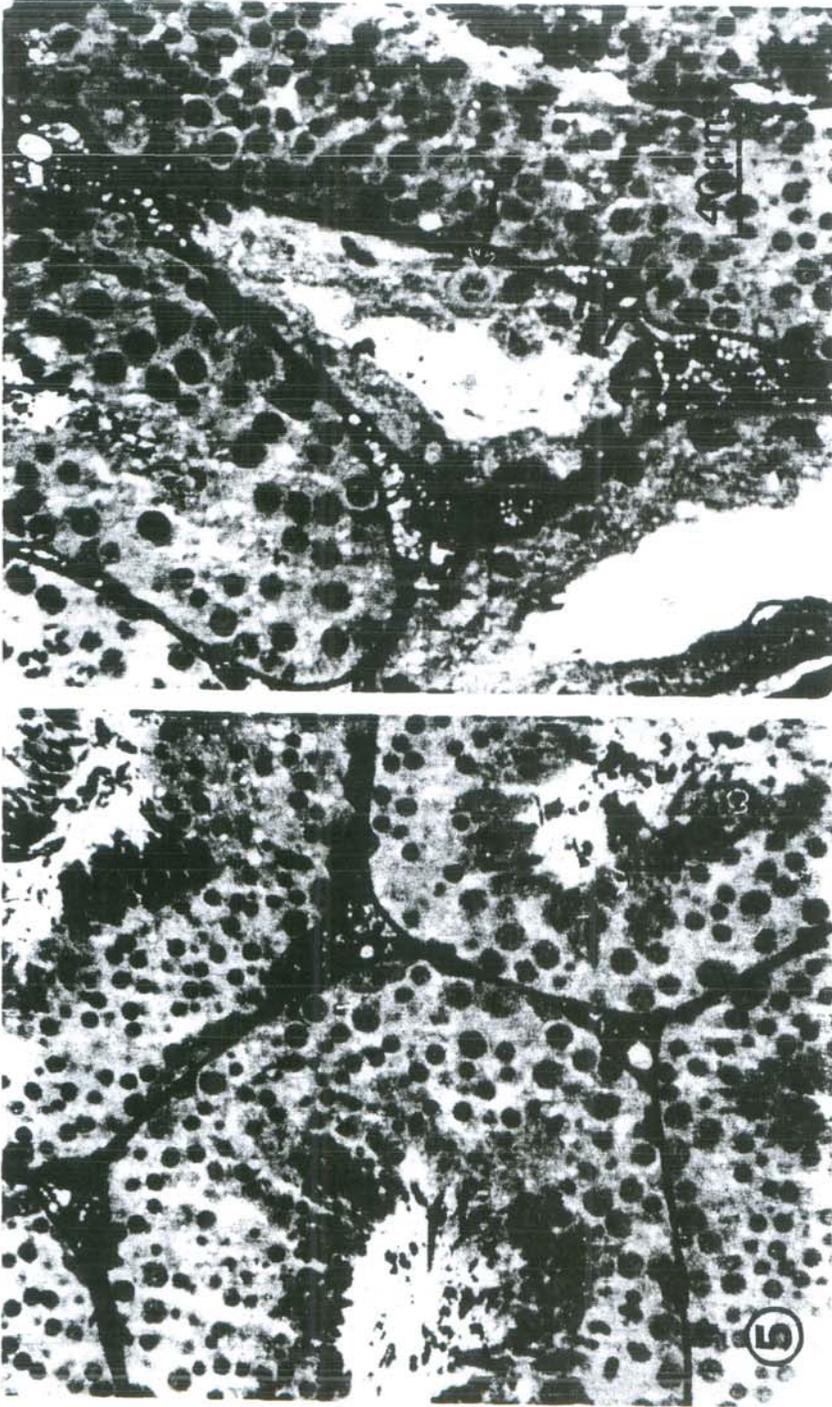


FIG. 5. Testis of control *Uta* in mid-June. Tubules contain all spermatogenic stages and sperm.

FIG. 6. Testis of irradiated *Uta* in mid-June. Some tubules show spermatogenic activity while others are lined by only Sertoli cells. Leydig cells are conspicuous in the intertubular areas. Abnormally large spermatogonia indicated by arrows.

had such damaged tubules. These effects occur in both 10-month-old males and in those over 22 months, but especially in lizards collected close to the source of radiation. In the June sample, testes of all the irradiated lizards (12 months old, and over 24 months) are grossly mottled, and there are few or no sperm in either the testes or epididymides.

The total gonadotropin content of the pituitaries, assayed by competitive radioreceptor assay, did not reveal clear differences between irradiated and control males in May (Fig. 7), indicating that the spermatogenic deficiencies were not due to a shortage in pituitary stores of this hormone.

Few spermatogonia are seen in the testis tubules of irradiated lizards, and when they occur they often appear anomalous. They are sometimes $30\ \mu\text{m}$ in diameter (twice the size of spermatogonia in controls), with a large, slightly eccentric nucleus (Fig. 6). Ultrastructurally, the cytoplasm of these cells may contain unusual concentrations of mitochondria and Golgi stacks. In contrast, spermatogonia of control testes usually have limited cytoplasm with few organelles.

Observations on the testicular interstitial tissue support the conclusion that pituitary gonadotropin production has not been affected by irradiation. In testes of irradiated *Uta*, Leydig cells are conspicuous, due in part to the reduced size of the testis tubules (Fig. 6); analysis of three control and three irradiated testes in June, however, shows that the absolute mass of Leydig cells is essentially the same in the testes of the two groups (Table I). In addition, despite individual variability within each group, plasma testosterone measurements for irradiated and control males are essentially the same (Fig. 7). Another measure of Leydig-cell activity in lizards is the enlargement of the renal sex tubules. These tubules

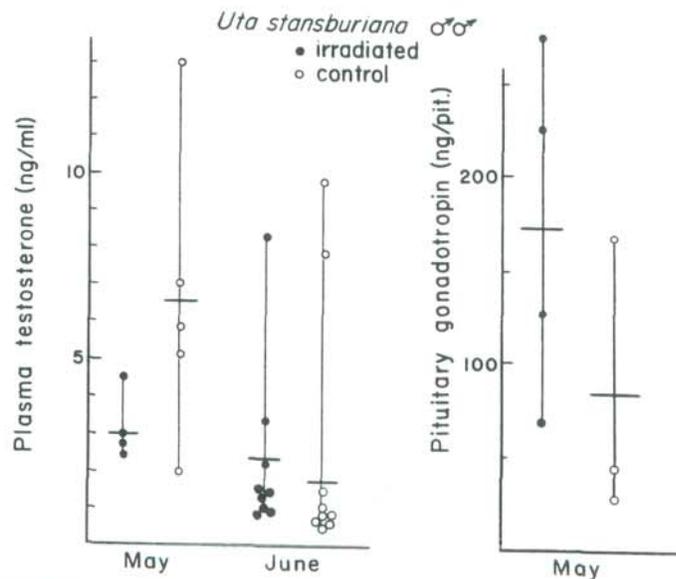


FIG. 7. Testosterone levels (determined by radioimmunoassay) and pituitary gonadotropin content (by radioreceptor assay) in irradiated and control male lizards. Vertical lines connect individual values, horizontal bars indicate averages.

TABLE I
Testis Function in Individual Irradiated and Control *Uta* in June^a

Treatment	Lizard	Plasma testosterone (ng/ml)	Weight left testis (mg)	LC (%) ^b	LC mg/testis	LC relative size ^c
Irradiated	95	0.883	11.0	2.78	0.31	7.95
	96	—	3.0	21.97	0.66	6.26
	97	1.53	7.3	9.70	0.71	10.30
Control	86	—	12.0	3.25	0.39	5.25
	87	1.19	16.0	3.50	0.56	7.79
	88	7.97	10.0	1.20	0.12	7.38

^a Leydig cell (LC) analysis for each lizard was based on 50 grid-fields under oil immersion, 400 points per field.

^b (Grid points on Leydig cells ÷ total grid points) × 100.

^c Number of grid points on Leydig cells ÷ number of LC nuclei in grid.

are equally developed in irradiated and control animals, further confirming that irradiation has not affected the androgenic function of the testis.

The ultrastructural morphology of the Leydig cells of *Uta* is similar to that of other vertebrates, with an abundance of agranular endoplasmic reticulum, many lipid droplets, and mitochondria with generally tubular cristae. The Leydig cells of control lizards contain more residual bodies, while those of irradiated lizards have more abundant lipid and more frequently show a Golgi apparatus. No clear correlations emerge between morphological characteristics of the Leydig cells and age of the lizard, plasma testosterone level, spermatogenic state of the testis tubules, or testis size (e.g., Table I).

Measurements of the height of the thyroid epithelium in several irradiated and control males from May and June showed no consistent differences between groups. In addition, plasma T_4 levels of six irradiated lizards collected in June did not differ significantly from those of six controls (mean ± SE for irradiated, 1.18 ng/ml ± 0.768; for control, 1.50 ng/ml ± 1.18).

A cytological comparison was made of the adrenal glands of nine irradiated and nine control males from April, May, and June. The nuclei of steroidogenic cells in four irradiated animals are significantly larger than those of three controls. In May and June there was no difference between the two.

Irradiated, Agonadal Females

Our evaluation of radiation effects on female *Uta* is limited to analysis of irradiated individuals lacking visible ovarian tissue, as described by Turner and Medica (4). Pituitaries from a total of 10 sterile females collected in April, May, and July were examined histologically or were used for hormone assay. The ultrastructure of the gonadotropes of two sterile females in April resembles that of the stimulated cells of castrated animals (Fig. 8). There are few secretion granules. An abundance of granular endoplasmic reticulum is organized in vesicles 0.5 μm in diameter, but also may occur in irregular swollen cisternae. Other characteristics of these cells are a large nucleolus, numerous small dense

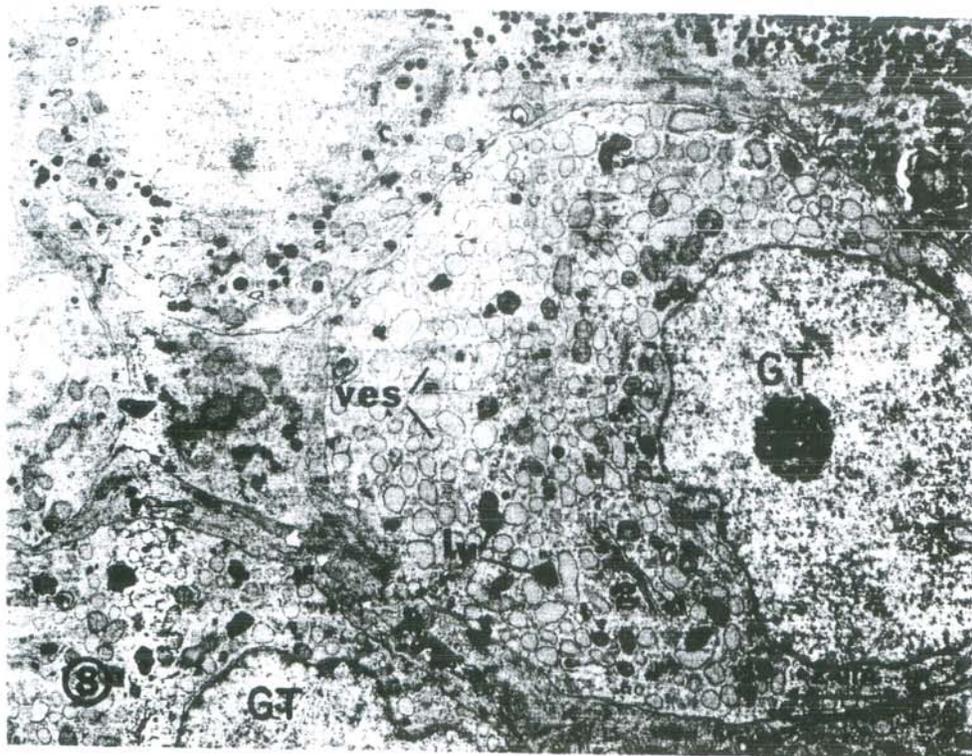


FIG. 8. Anterior pars distalis of an irradiated female lizard whose ovaries were resorbed. The gonadotropes (GT) are degranulated and the cytoplasm is filled with vesicles of granular endoplasmic reticulum (ves). Lysosome (ly); Golgi area (g).

lipofuchsin bodies, frequent long stacks of Golgi saccules and their vesicles, myelin figures, elongated mitochondria, and occasional lysosomes and cytosegasomes.

The gonadotropes in sterile females in July generally contain more secretion granules than do those in April, although the cells still appear hyperactive, with many expanded cisternae. Golgi stacks are shorter and less common than earlier in the spring.

The gonadotrope is the most drastically altered cell type in the pituitaries of sterile females. Another cell that appears relatively active occurs primarily in the anterior part of the PD and has uniformly large and dark secretion granules, often with a small projection. This cell is morphologically similar to the proposed prolactin-producing cells of *Anolis* (8). In sterile female *Uta* these cells have many large lysosomes, but in addition there are large Golgi areas with many small vesicles containing an osmiophilic material near the maturing face of the Golgi saccules. Some of these cells have extensive arrays of flattened cisternae lined by granular endoplasmic reticulum, while others seem relatively quiescent.

The pituitary gonadotropin content of three sterile females in May (average, 52.6 ng/pit; range, 34.2–62.5) is low compared to four female controls (average, 220 ng/pit; range, 128–308) or to two irradiated females still having gonads (208 and 376 ng/pit). The values for the sterile females are similar, however, to

the lower values of control males at this time (see Fig. 7), in which the gonadotropes are synthetically active.

Measurements of the thyroid epithelium in three sterile females collected in May are smaller than those of five of six males (two irradiated and four control) at this time, but the difference is not statistically significant.

The steroidogenic tissue in the adrenal glands of sterile females also appears to be relatively inactive (Table II). In May the nuclei of steroidogenic cells of three sterile females are significantly smaller than those of all other groups measured. Nucleolar diameters in the same nuclei were also 10% smaller in the sterile females, a difference significant at the same level.

A characteristic of agonadal females is the accumulation, especially during the breeding season, of large quantities of orange-yellow fat in the abdominal fat pads (2, 4). An excessive amount of fat also occurs about the thyroid gland in these animals, and there is a great accumulation of lipoidal material within the cells of the liver.

DISCUSSION AND CONCLUSION

Testicular impairment in males subjected to sustained low-dose irradiation involves primarily the spermatogenic process; the steroidogenic activity of the interstitium (Leydig cells) appears essentially normal as judged by the appearance of androgen-dependent accessory sexual structures, levels of circulating testosterone, pituitary gonadotrope cytology, and the ultrastructure of the Leydig cells themselves. The normal appearance and gonadotropin content of the pituitary suggest that spermatogenic abnormality results from direct effects of irradiation on gonads rather than from pituitary hormone deficiency. Histology of the testes of *Uta* indicates that spermatogonia are the cells affected by radiation. This is not unexpected, since mammalian germ cells (both male and female) have been shown to be most susceptible to radiation-induced death during the last premeiotic stages (12).

Depletion of the germinal epithelium through damage to spermatogonia and maturation of later, more radioresistant spermatogonial stages is usual in mammals subjected to a single moderate dose of radiation (13). Recovery follows within weeks as the testis tubules are repopulated by surviving spermatogonia. Single-dose exposures of male *Uta* to 500 R of X radiation also resulted in temporary sterility, with complete recovery in 36 days (14). Under sustained irradiation, such as at the Nevada study site, however, attrition of spermatogonia continues and spermatogenic recovery apparently does not occur within the breeding season. From data supplied for *Xantusia vigilis* (15), 50,000 seems a reasonable estimate of the number of spermatogonia in a single inactive testis; during active spermatogenesis this number is greater by a factor of at least 10. The absence of sterile male *Uta* in spring is evidence that enough spermatogonia survive irradiation during the breeding season to repopulate the testis tubules in the winter months when this lizard spends more time underground. Such seasonal behavioral modification results in some shielding from radiation: Between September and May tissue doses to *Uta* are about 35% of free-air exposure, whereas during the summer months almost all incident radiation is absorbed (16).

TABLE II
Relative Nuclear Size of Adrenal Steroid Cells in Control and Irradiated Lizards,
Based on Weights of Camera Lucida Tracings

Group	April			May			June		
	No. of lizards	No. of nuclei	Weight (mg) ^a	No. of lizards	No. of nuclei	Weight (mg) ^a	No. of lizards	No. of nuclei	Weight (mg) ^a
♂ Control	3	30	2.15 ± 0.116	3	31	2.70 ± 0.092	3	20	2.80 ± 0.130
♂ Irradiated	4	43	3.22 ± 0.112 ^b	3	30	2.57 ± 0.129	2	20	2.77 ± 0.101
♀ Control				3	25	3.52 ± 0.166			
♀ Sterile (irrad.)	2	20	2.31 ± 0.088	3	30	1.73 ± 0.089 ^b			

^a Mean ± standard error.

^b Different from control of the same sex ($p < 0.05$).

The reaction of female lizards to conditions of sustained low-level radiation differs from males in that there is more complete gametogenic arrest. In birds and mammals the process of oogenesis is completed near birth or hatching, and a large number of germ cells for future ovarian activity exist as oocytes at this time. In lizards, however, clusters of oogonia continue to give rise to oocytes by mitotic division through sexual maturity (17). There are a limited number of oogonia concentrated in one or two germinal beds in the saurian ovary. In *Uta* we estimate only about 500 such cells in each of two germinal beds in an ovary. The radiosensitivity of this class of mitotically active cell and their small number make them particularly vulnerable to extinction. On the irradiated plot a few female *Uta* have been found with one resorbed and one functional ovary. Such individuals suggest that irradiation damage to ovarian germinal beds is gradual, and that the maintenance of an ovary depends on elements within the ovary itself; i.e., hormones from the contralateral ovary do not support ovarian tissue in an ovary in which the oogonia have been destroyed.

Contrary to male *Uta* in which damage to the germinal epithelium does not affect steroidogenesis, there is reduction or complete loss of gonadal steroidogenic activity in affected females. Atrophy of oviducts and the appearance of typical "castration" cells in the pituitary suggest greatly reduced levels of sex steroids (estrogen?). The apparent reduction in pituitary gonadotropin content in sterile females compared with controls probably reflects the increased secretion rate (i.e., reduced storage) in the former, due to removal of inhibitory feedback from gonadal steroids. Thus, as in males, it seems unlikely that gonadal atrophy or impairment is due to pituitary damage. The dramatic increase in stores of fat in agonadal females may well represent energy saved by virtue of the lack of reproductive effort (18, 19); absence of the gonads could well be responsible for the modified fat metabolism of sterile females as well as for an apparently diminished activity in thyroids and adrenals.

Assays of hormone levels and cytological observations on pituitaries and gonads support the conclusion that reproductive impairment in *Uta* subjected to chronic low levels of radiation results primarily from direct damage to radiosensitive elements in gonadal tissue rather than from interference with pituitary gonadotropin production and secretion. Irradiation effects a gradual reduction in the number of spermatogonia in the testis tubules, but due to the abundance of these cells there is only a tolerable reduction in fertility in males. The endocrine function of the testis remains essentially normal and pituitary cytology is unaffected. In contrast, a limited supply of radiosensitive oogonia results in severe irradiation effects in females, with complete resorption of ovarian tissue, including steroidogenic elements. In the absence of controlling gonadal steroids in affected females, pituitary cytology is altered, primarily by hypertrophy of the gonadotropes.

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