

Sterility among Female Lizards (*Uta stansburiana*) Exposed to Continuous γ Irradiation¹

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A natural population of the lizard *Uta stansburiana* occupying a fenced 9-ha area in southern Nevada was exposed to essentially continuous γ irradiation from an artificial source between February 1964 and September 1973. Tissue doses were estimated using implanted lithium fluoride microdosimeters. Females became sterile as early as 11 months of age, but many were still fertile at ages of 20 months and a very few may have reproduced at 32 months. Dosimetry showed some females to be sterile after accumulated doses of around 500 rad, while others may have required 1000 or more rad. One female estimated to have received over 1200 rad was still reproductive. Irradiated females may pass through a state of half sterility, during which time they possess one functional ovary. Female *U. stansburiana* are sterilized at lower doses than the sterilizing dose (1500 rad) previously suggested for the leopard lizard, *Crotaphytus wislizenii*.

INTRODUCTION

Populations of lizards occupying a continuously irradiated 9-ha enclosure in southern Nevada were studied between 1964 and 1973 (1-4). Animals were exposed to γ radiation from a centrally located cesium source atop a 15-m tower (5, 6). The strength of the radiation source was 33,500 Ci when it was activated in January 1964. Because the source was differentially shielded in an attempt to create a uniform field of radiation, free-air exposure rates early in the experiment ranged from about 10 R/day near the center of the enclosure to around 2 R/day at the periphery (6). By 1973 the decay of the source reduced free-air exposure rates to around 8 R/day close in and 1.5 R/day at the edge (7).

Tissue doses to animals occupying the irradiated enclosure were always less than exposure rates, often markedly so. Using attached lithium fluoride dosimeters, French *et al.* showed that annual doses to pocket mice (*Perognathus formosus*) were about 360 rad, with most of the dose received during the spring and summer (8). Turner and Lannom measured doses with dosimeters implanted beneath the skin of lizards and estimated that tissue doses sustained by *Uta stansburiana* were from 0.3 to 0.6 of exposure rates (9). Comparable figures for

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whiptail lizards (*Cnemidophorus tigris*)—with a shorter period of above-ground activity—were around 0.1 to 0.2. Doses to leopard lizards (*Crotaphytus wislizenii*) were intermediate to the foregoing species. Turner *et al.* gave more refined estimates for *Uta* in the enclosure, judging that annual doses ranged from as high as 1800 rad near the center to around 360 rad at the periphery (1). Most animals were estimated to receive around 750 rad/year. Later, Turner *et al.* estimated annual tissue doses to leopard lizards as around 450 rad, and to whiptails as 200–250 rad (2).

Performances of irradiated populations of lizards were compared with those of similar populations occupying three nearby control areas, two fenced and one unfenced. By 1968, there was evidence of reproductive failure among leopard lizards and the investigation of this situation has been previously described (2, 4). Basically, the effect of continued exposure to γ radiation was sterility among females, manifested by an apparently complete loss of ovarian tissue and pronounced hypertrophy of pleuroperitoneal fat bodies. We also found this effect among irradiated female whiptail lizards (2) and horned lizards (3), but never among control animals from nearby areas. Sterility among irradiated female lizards has been more widely manifested than in males, and appears to be of greater importance in terms of the survival of the populations.

The responses of various populations of lizards to continuous irradiation represent a complex interaction between the specific demographic regimens of the lizards (particularly age at maturity and natural life span) and the cumulative stress. A number of questions may still be raised concerning details of these interactions, as well as possible compensating mechanisms. For example, the manner in which female sterility develops is not clear. All female lizards examined between 1969 and 1971 exhibited complete loss of ovarian tissue, and we could only draw indirect inferences as to when this condition was first manifested. We had no information as to how sterility developed over time; whether gradually or quickly. Whereas all female horned lizards and leopard lizards in the irradiated enclosure were sterilized, this was not true of female whiptails and *Uta*. We lacked information on the proportion of females affected, and how sterility was related to age and accumulated radiation exposure. This paper is addressed to these questions, insofar as they could be investigated in the population of *Uta* occupying the irradiated enclosure.

METHODS

One part of this study involved marking a large cohort of newly hatched female *Uta* in the summer and early fall, when these animals were 1–2 months of age. This was accomplished in the summer of 1972, when 270 female hatchlings were captured in the irradiated area, marked by toe clipping, and released at points of capture. We then removed small numbers of individuals from this group each month until the cohort was exhausted by sampling and normal attrition. Female *Uta* of similar ages were collected outside of the irradiated plot and served as controls. The first samples of females were taken in September 1972, and sampling continued on a monthly basis (except for December 1972) until the fall of 1973, when it was no longer profitable to seek out marked animals. Each sample was

made up of from one to five females of known ages, and a total of 32 females was taken from the irradiated area during the course of the experiment. At the same time, 36 females were collected as controls.

All animals were measured, weighed, and autopsied. Weights of ovaries and eggs (if present), oviducts, and fat bodies (if present) were determined using a Mettler Gram-atic analytical balance. We also computed ratios of ovary and fat body weights to live body weights.

We estimated accumulated radiation doses to lizards in the irradiated area by implanting lithium fluoride microdosimeters beneath the skin. General procedures have been described previously (9, 10). In general, we did not place dosimeters in lizards <25 mm in snout-vent length (or <0.5 g), because dosimeters were often lost from such small animals. Dosimeters were removed from lizards as opportunities arose; some dosimeters were removed within a week and others remained in place over the winter and were not retrieved until >200 days after implantation. Recovered dosimeters were sent to their manufacturer, Edgerton, Germeshausen and Grier, in Santa Barbara, California. Here they were read, and readings converted to estimates of tissue doses (in rad) by multiplying by 0.96. Tissue doses were compared to total exposures, taking into account the time between implantation and removal and each lizard's location within the irradiated area. We used an isodose map of the area based on 1973 measurements to estimate each individual's exposure (7). Allowances were made for 45 days of inactivity during the winter and for days when the radiation source was inactivated (usually about 5 days monthly). For each animal, a ratio (K) was computed as the total free-air exposure (R) divided by the corresponding dosimeter reading (in rad). Values of K tended to increase with time, as was true in dosimetry studies of leopard lizards (2). Dosimeters retrieved after 50 days or more registered lower doses (relative to estimated exposures) than dosimeters recovered after shorter time periods. This would occur if there were loss (or fading) of the thermoluminescent properties of the exposed dosimeters. We examined this problem by regressing values of K on time, d (in days). First, we analyzed all of our dosimetry records ($n = 92$) with values of d ranging from 7 to 255. Second, we analyzed only those records with $d \leq 50$ ($n = 46$). These tests indicated that dosimeters left out for more than 50 days underestimated actual tissue doses, so we used only those records with $d < 50$ as estimators of K . The mean value of K based on 46 records was 1.46. We were then able to calculate, for each female, expected tissue doses based on the animal's location within the enclosure and the duration of exposure. The best estimate of tissue dose, T , in terms of exposure, E , was:

$$T = 0.685E$$

Medica *et al.* showed that reproductive states of female *Uta* may be inferred by palpation.² One can discriminate between ovaries with no follicles (or very small ones) and ovaries with follicles 2 mm or greater in diameter, as well as between follicles and eggs. The data given by Medica *et al.* showed that fairly good estimates of the numbers of follicles can be made. Furthermore, it is possible

² P. A. Medica, G. A. Hoddenbach, and J. R. Lannom, Jr., *Lizard Sampling Techniques*. Rock Valley Miscellaneous Publ. No. 1, 55 p., 1971.

to determine the absence of ovaries and the presence of increased amounts of body fat by palpation. Because we were interested in the incidence of sterility among female *Uta* of different ages, Medina examined 155 irradiated females during the spring of 1972 and 126 females during the spring of 1973. Animals were scored as normal or sterile (on the basis of palpation) and assigned to two age groups (8-11 months and 20+ months) on the basis of body size (11).

RESULTS

Table I summarizes basic data pertaining to irradiated females marked during the summer and fall of 1972 and removed during the next year, as well as comparable figures for control animals collected over the same period of time. Female *Uta* born in the irradiated plot possess ovaries and oviducts of normal size. These organs were also normal in color and appearance. Some development occurs during the fall and winter, but real growth does not commence until the ensuing spring. Then weights of ovaries and oviducts increase quickly and egg production by irradiated females 8-9 months of age occurs in an apparently normal fashion. The eight females taken from the irradiated area between March and June 1973 (Table I) exhibited, when autopsied, ovaries with yolked follicles or, in one case, oviducal eggs. However, the last five females taken from the irradiated plot (between July and September 1973) were either sterile or half sterile.

We first analyzed live body weights of irradiated and nonirradiated animals. Females differed in their reproductive states; some had ovaries with enlarged follicles while others bore eggs. In order to eliminate this source of variation we adjusted the body weights of seven females with eggs by subtracting the weights of the eggs. Irradiated and control females were grouped into three time periods: September-November, January-April, and May-September. A factorial analysis of variance of these data was performed. Although there was a pronounced time

TABLE I
Live Body Weights and Wet Weights of Ovaries, Fat Bodies and Oviducts of
Irradiated (I) and Nonirradiated (NI) Female *Uta*^a

Month	n		Mean body weights (g)		Mean ovary weights (mg)		Mean fat body weights (mg)		Mean oviduct weights (mg)	
	I	NI	I	NI	I	NI	I	NI	I	NI
September	5	5	1.31	1.39	1.6	1.2	0.2	9.2	—	—
October	3	3	1.77	2.09	2.7	4.0	1.3	30.0	—	—
November	3	2	1.58	2.16	3.7	6.0	7.0	33.0	1.0	<1.0
January	4	5	1.92	2.04	5.5	6.0	21.0	23.0	2.5	3.0
February	4	3	1.98	1.92	8.0	8.0	13.0	14.0	3.8	6.0
March	1	2	2.80	1.69	25.0	8.0	35.0	1.0	16.0	3.0
April	2	2	2.81	2.04	356.0	52.0	7.0	14.0	50.0	27.0
May	4	4	3.28	3.69	474.0	192.0	2.0	8.0	59.0	—
June	1	3	4.35	3.83	523.0	13.0	1.0	11.0	45.0	21.0
July	1	4	3.86	3.52	Sterile	4.0	305.0	105.0	13.0	15.5
August	2	3	3.30	3.75	Sterile or half sterile	4.0	247.0	211.0	14.0	14.0
September	2	0	2.85	—	Half sterile	—	142.0	—	11.0	—

^a Animals were taken in Rock Valley between September 1972 and 1973. Those collected in September 1972 were 1-2 months of age; those taken in August and September 1973 were 13 and 14 months old, respectively.

TABLE II

Mean Ratios of Ovary Weights (mg) to Live Body Weights (g) among Irradiated and Nonirradiated Female *Uta stansburiana* Collected between September 1972 and 1973

Time period	Irradiated			Nonirradiated		
	n	Mean O/B	Range	n	Mean O/B	Range
September–November 1972	11	1.61	0.90–2.89	10	2.02	0.65–5.73
January–April 1973	10	4.77	2.67–10.99	11	4.09	1.80–10.10
May–June 1973	2	3.95	0.81–7.09	6	5.47	3.46–8.47

effect, the F ratios associated with treatment and interaction between time and treatment were insignificant.

We next considered the weights of ovaries of nonirradiated and irradiated females. As can be seen from Table I, ovary weights of both groups increased from around 1–2 mg in very young females (1–2 months), to some hundreds of milligrams during the spring, and then declined to around 4 mg in the fall. Did changes in the relative weights of ovaries of irradiated females decline before sterility occurred? To explore this question we computed ratios of ovary weights in mg (O) to live body weights in g (B). Body weights were adjusted by subtracting weights of eggs. Seven females with enlarged follicles were omitted, and the four sterile or half sterile females taken from the irradiated area could not be used. Irradiated and control animals were grouped into three time periods: September–November, January–April, and May–September (Table II). Analysis of variance of these data indicated a highly significant time effect, but the F ratios associated with treatment and interaction were insignificant. Hence, our data showed similar trends in values of O/B among all nonsterile lizards examined.

We analyzed ratios of fat body weights in mg (L) to live body weights (L/B) in a similar manner. Animals were grouped according to time of collection as in the previous analysis, and mean values of L/B computed (Table III). Analysis of variance showed that most of the observed variation was due to time, but interaction of treatment and time was also highly significant. The main point is that relative weights of fat bodies of all irradiated females increased in the fall of 1973. Of the 10 control females collected between June and August 1973, three had fat bodies of about the same relative size as irradiated animals and the other seven had smaller ones. We consider the difference between the two groups a radiation effect, and this observation is in accord with previous work showing all sterile females of *Crotaphytus wislizenii* and *Cnemidophorus tigris* to possess enormously hypertrophied fat bodies (2).

When does sterility, or half sterility, first occur, and how is this related to accumulated tissue doses? Table IV lists 13 females of known age taken from the irradiated area between March and September 1973, and gives estimated tissue doses sustained by these animals based on their locations within the area. Although all five individuals 12 months and older were affected, we know that sterility does not always occur so early in life. Many irradiated females reproduce in their second year. Table V gives data pertaining to females still reproducing at

TABLE III

Mean Ratios of Fat Body Weights (mg) to Live Body Weights (g) among Irradiated and Nonirradiated Female *Uta stansburiana* Collected between September 1972 and 1973

Time period	Irradiated			Nonirradiated		
	n	Mean L/B	Range	n	Mean L/B	Range
September–November 1972	11	3.33	0 – 8.07	10	10.70	0 – 22.57
January–April 1973	10	8.76	3.19–16.90	11	7.14	0 – 16.16
May–September 1973	6	54.01	0 – 86.96	13	21.17	0.81–75.19

known ages of 20+ months. This information is based on palpation of live animals occupying the irradiated area during 1972 and 1973 (see above). Apparently sterility among *Uta* within the irradiated area can occur as early as 11–12 months of age, but *after* the animal reproduces in its first breeding season. Sterility may occur at any time after 12 months; some females were sterile at age 20 months and others were still reproductive. Although a few females may begin their third reproductive season (Table V), almost all animals 32 months of age or older ($\leq 5\%$ of the population) were sterile. Some females may be completely sterilized by accumulated doses of around 500 rad, yet one lizard (3397, Table V) apparently sustained a dose of over 1200 rad and still showed signs of reproductive activity. This last lizard evidently spent its entire lifetime in a rectangular area about 24×30 m, over which the free-air exposure rate ranged from 2.3 to 3.7 R/day. The loss of one ovary may be brought about by less than fully sterilizing doses. This condition may persist for some time and the single ovaries of half sterile females may remain functional.

TABLE IV

Reproductive States of 13 Female *Uta stansburiana* Taken from the Irradiated Area between March and September 1973, and Estimated Accumulated Tissue Doses

Animal number	Month removed from area	Age when removed (months)	Condition	Estimated tissue dose (rad)
9495	March	8	2-mm follicles	240
9713	April	9	2-mm follicles	418
9986	April	9	6-mm yolked follicles	411
9146	May	10	Oviducal eggs	343
9116	May	10	7-mm yolked follicles	406
9594	May	10	6-mm follicles	326
9988	May	10	4-mm follicles	306
9721	June	11	6-mm follicles	341
9941	July	12	Sterile	456
9629	August	13	Sterile	622
9114	August	13	Half sterile	301
9141	September	14	Half sterile	534
9692	September	14	Half sterile	326

TABLE V

Reproductive States of Seven Female *Uta stansburiana* 20+ Months of Age Examined in the Irradiated Area in 1972 and 1973, and Estimated Accumulated Tissue Doses

Animal number	Date examined	Age (months)	Reproductive condition inferred from palpation	Estimated accumulated tissue dose (rad)
3351	March 14, 1972	20	5-mm follicles	628
	April 17, 1972	21	5-mm follicles	
	March 19, 1973	32	3-mm follicles	
3359	March 15, 1972	20	Eggs	749
	April 26, 1972	21	Eggs	
3376	April 12, 1972	21	3-4-mm follicles	542
	April 28, 1972	21	Eggs	
3397	April 12, 1972	20	5-6-mm follicles	1273
	March 30, 1973	31	6-mm follicles	
4164	March 16, 1973	20	2-3-mm follicles	728
4165	March 16, 1973	19	2-3-mm follicles	790
	April 9, 1973	20	Eggs	
4192	April 2, 1973	21	6-mm follicle ^a	820

^a Possibly impaired.

The apparent variability in relationships between sterility and age and accumulated doses is not easy to reconcile. Aside from differences in individual radiosensitivity, we can identify two sources of error. First, the home ranges (and locations) of lizards are not always reliable guides to radiation exposures because animals may make occasional movements not reflected by recapture loci. Second, relationships between estimated exposures and tissue doses (K) vary. When we analyzed this relationship based on 46 readings, the correlation coefficient was only +0.517. Irregularities in terrain and/or behavioral differences among animals contribute to this source of error.

The data reviewed so far indicate that, for various reasons, female *Uta* become

TABLE VI

Incidence of Sterility among Two Age Groups of Female *Uta* in the Irradiated Plot during 1972 and 1973^a

Condition	1972		1973	
	Adults (20+ months)	Yearlings (8-11 months)	Adults (20+ months)	Yearlings (8-11 months)
Normal	20 (50.0)	109 (94.8)	16 (55.2)	88 (90.7)
Sterile	20 (50.0)	6 (5.2)	13 (44.8)	9 (9.3)

^a Condition was inferred by palpation of live animals. Numbers in parentheses indicate percentages of each age group sterile and normal.

sterile at different ages after 11 months. Some females are unable to reproduce at an age of 20 months and others are still fertile. We believe that almost all females 32 months old are sterile. To understand the dynamics of such a population we need to know the incidence of sterility among 20-month old females. During the spring of 1972 and 1973 Medica evaluated the condition of female *Uta* of different ages in the irradiated plot. This survey was based on palpation of live animals which were then released.

Table VI summarizes this information. These data show that yearling females are rarely sterile (and the affected animals were probably 11 months old). Roughly half of the older females were judged to be sterile. If we assume that 83% of the animals 20+ months of age were 20 months old and 17% were older (11), and that all females 32+ months of age were sterile, we can estimate the incidence of sterility among 20-month old females. Of the 69 females 20+ months of age in Table VI, we would expect about 57 to be 20 months old. All of the 12 older females would presumably be sterile. Then 21 of 57 (37%) 20-month old lizards were sterile.

DISCUSSION

When female sterility among leopard (*Crotaphytus wislizenii*) and whiptail lizards (*Cnemidophorus tigris*) was evaluated, it was stated that, ". . . an accumulated dose of around 1500 rads was sufficient to destroy the ovary. . . . This estimate could be wrong by a few hundred rads, and it would undoubtedly vary between individuals" (4). Our findings with respect to *Uta stansburiana* indicate that sterility is brought about by lower doses, perhaps 500 rad in some cases, but also that other females may sustain doses of up to 800-1200 rad and remain reproductive. It is certainly possible that the two species of lizards (*Crotaphytus wislizenii* and *Uta stansburiana*) in which female sterility has been analyzed most intensively may differ in their radiosensitivity. This is hard to evaluate because of the wide range in dose-response relationships among irradiated female *Uta*. Because of several sources of error in the *Uta* data, we are not dealing entirely with variations between individual lizards. It is unlikely that the time of autopsy of an animal coincided exactly with the onset of sterility, but "accumulated doses" were computed to time of death. We have also commented on the problems of dosimetry among animals free to move about in their natural environment. We also point out the possibility that differences in dose rate could have some effect on the relationship between accumulated doses and sterility.

It is not obvious how this problem could be evaluated under controlled conditions in the laboratory, for it is difficult to sustain *Uta* in cages for the period of time (say, 12-24 months) necessary to accumulate sterilizing doses from continuous exposure to a few rad per day. We do not know how the ovaries of adult female *Uta* would respond to the acute administration of 600-1500 rad of γ radiation. Some females survived (for 30 days) doses exceeding 2000 rad in acute irradiation experiments but no autopsies were performed (12).

In spite of the variability in responses described above, it is clear that the capacity of the *Uta* population to withstand chronic radiation stress is markedly better than that of populations of leopard lizards and horned lizards. We have

commented on this point previously (2, 4), but reiterate that the principal advantage enjoyed by *Uta stansburiana* is its early sexual maturation (8-9 months) and the ability of yearling lizards (which make up around 75% of spring populations) to reproduce normally before damaging doses of radiation are accumulated. Turner suggested that compensatory changes in early survival could also protect the population from reductions in fertility associated with sterility of some older females (4). A model was postulated assuming half the 20-month old females to be sterile (cf. 37% estimated in this paper). In contrast to *Uta*, populations of leopard and horned lizards in the irradiated plot have declined in numbers because of complete failure of reproduction. These lizards are not normally mature until 20-21 months of age and breeding populations are principally composed of older animals. The Rock Valley experiment showed that populations with these demographic attributes are much more vulnerable to continuous exposure to sublethal radiation stress.

French *et al.* reported on a 5-year study of populations of heteromyid rodents occupying the irradiated enclosure and three control plots (6). Although the four areas sustained differing densities of rodents, there was general synchronization of population fluctuations. Of four species of rodents studied, the pocket mouse (*Perognathus formosus*) exhibited the highest densities and French and his co-workers gave particular attention to this species. The irradiated population of *P. formosus* sustained numbers throughout the experiment, and afforded no obvious evidence of impaired reproduction. In April 1970 one male and one female were removed from the irradiated area and autopsied. Histological comparisons of their gonads were made with those from two animals from a control enclosure. Testes of both males had high sperm concentrations and were reproductively active. Ovaries of both females were reproductively active and contained new corpora lutea. Ovaries of the irradiated female also showed a large number of atretic follicles, but this was judged an effect of age rather than irradiation. The lifetime accumulated radiation dose to the experimental female was estimated to be about 1880 rad (6). These data suggest that ovaries of female pocket mice may be resistant to accumulated radiation doses sufficient to sterilize female lizards, and the long-term histories of the respective populations also support this view. If this be true we have no radiobiological explanation other than to suggest a more efficient capacity for recovery by ovaries of pocket mice exposed to continuous doses of a few rad per day.

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