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OVARIAN CYCLE OF THE MOUNTAIN SPINY LIZARD

SCELOPORUS JARROVI COPE

by

Stephen Robert Goldberg

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GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my

direction by Stephen Robert Goldberg

entitled   OVARIAN CYCLE OF THE MOUNTAIN SPINY LIZARD

SCELOPORUS JARROVI COPE

be accepted as fulfilling the dissertation requirement of the

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SIGNED: *Stephen Robert Spielberg*

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ABSTRACT

Collections of Sceloporus jarrovi were made over a
four year period. Histological and weight variations are
recorded for seasonal changes in the ovaries and fat bodies.
The ovaries undergo a seasonal cycle in which yolk deposi-
tion occurs in September-October and is followed by ovula-
tion in late November. The corpora lutea which form after
ovulation remain until parturition after which time they
degenerate rapidly. Follicular atresia is common during
the winter months, less common during the spring and absent
during summer and early fall. Fertilization takes place
soon after ovulation with embryonic development suspended
at the blastoderm stage until April. Formation of allanto-
placentae and omphaloplacentae occurs in late March. Young
are born in mid-June after a gestation period of roughly
seven months. Sperm may remain in vaginal epithelial
pockets until as late as April (seven months after insemina-
tion). Fat bodies are at maximum sizes in early autumn;
minimum sizes occur in the spring and recrudescence is com-
pleted by July. Females accumulate higher fat reserves in
early autumn than do males; this extra fat is presumably
utilized during vitellogenesis.

INTRODUCTION

This work marks the completion of an intensive
study on the breeding biology of the viviparous mountain
spiny lizard <u>Scoloporus jarrovi</u> Cope which is common at
elevations above 4,000 feet in several mountain ranges
in southeastern Arizona (Lowe 1964). The taxonomy and
distribution of this polytypic species was revised by
Chrapliwy (1964). The subspecies <u>Sceloporus j. jarrovi</u>
under investigation in this study ranges from southeastern
Arizona, southward to the Mexican state of Durango. Other
subspecies extend as far south as Hidalgo (<u>Sceloporus j.
immucronatus</u>) and Guanajuato (<u>Sceloporus j. minor</u>). Short
notes on the reproductive habits of <u>Sceloporus j. jarrovi</u>
were contributed by Zweifel (1949) and by Carpenter (1960).

While information on the reproduction of North
American lizards is accumulating at increasingly rapid
rates, there are still groups among which our knowledge
of this subject is fragmentary. Reproductive studies on
viviparous North American lizards have been contributed
by Miller (1948) and Heimlich and Heimlich (1950) on
<u>Xantusia vigilis</u>, and by Crisp (1964) on <u>Sceloporus
cyanogenys</u>. Other noteworthy works on reproduction in
viviparous lizards include Weekes (1927a, 1927b, 1929,

1930, 1935) investigations of placentation in Australian lizards and Boyd's (1940, 1942) studies on the New Zealand gecko Hoplodactylus maculatus. Tinkle (1967) summarizes recent advances in these and related areas.

METHODS

Measurements of seasonal changes in the ovaries, oviducts and fat bodies were made for samples of Sceloporus jarrovi collected alive monthly (by noosing) over a 19 month period (April 1968-October 1969) and irregularly over a four year period (beginning in 1964) at Kitt Peak, elev. 6,700 ft., in the Quinlan extension of the Baboquivari Mountains, 53 miles southwest of Tucson, Pima County, Arizona.

Data tabulations made after recording weights of the above organs from a torsion balance, and weights of live lizards from a Mettler balance, are reduced and illustrated in the form of graphs or regression lines.

Tissues were fixed in Bouins or in 10% formalin, sectioned at 10 micra and stained with Heidenhain's iron hematoxylin. The photomicrographs were taken with a Zeiss photomicroscope.

Averages of the widths of 20 square fat cells measured through an ocular micrometer for each of eight males and eight females from the months January, April, July and October are graphed to depict the seasonal fat cycle.

Measurements of corpora lutea and follicle lengths were made with venier callipers, to nearest .01 mm.

Data for graphs showing seasonal changes in ovaries and fat bodies are expressed as percentages of total body weight.

Raw data is given in Appendices A-C.

THE OVARY

Gross Morphology

The ovaries of Sceloporus jarrovi are round to oval
shaped bodies located posteriorly in the body cavity where
they are suspended by mesenteries attached to the dorsal
body wall. The morphology varies depending on the time of
year that they are examined. The ovaries attain their
greatest weight during the autumn months prior to ovula-
tion (Fig. 1, Tables 1-4) when large quantities of yolk
gradually appear in the follicles. During this period the
ovaries consist of 1-6 large yolky follicles which may
range from 4-9 mm in diameter (Table 3) depending on the
month examined.

Ovaries examined from December females that under-
went a recent ovulation (Table 3) consist of (1) several
small follicles, less than 2 mm in diameter, and (2) from
0-4 secretory corpora lutea that show a progressive size
decrease (Tables 5-6) through the winter and spring.

Except for the gradual disintegration of the corpora
lutea (Tables 5-6), the morphology remains relatively con-
stant (December-June) until July when a rapid growth and
proliferation of follicles occurs.

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Histology

The ovarian elements of Sceloporus jarrovi include
seasonally varying numbers of follicles (Tables 3-4),
corpora lutea (Tables 5-6), and atretic follicles inter-
spersed in an ovarian stroma composed largely of colla-
genous fibers, with scattered fibroblasts and limited areas
of vascularization. The ovary is bordered on its periphery
by one layer of squamous epithelial cells.

Germinal epithelium is restricted to a few small
isolated masses near the dorsal surface of the ovary and
contains primary oogonia and oocytes in different stages
of development (Fig. 2). This tissue is most abundant
during periods of follicular maturation (June-August) and
is uncommon in the post-ovulatory, pre-parturition organ
(December-June).

The central mass of the growing and mature follicle
is filled with the primary oocyte which is characteristically
surrounded by a thin, homogeneously densely staining vitel-
line membrane. Directly outside the vitelline membrane is
a two-layered zona pellucida (Fig. 3) as in other verte-
brates. The outer layer of the zona pellucida is uniform-
ally densely staining. The inner layer is clear with
horizontal striations. It is referred to as the zona
radiata in this study and by Loyez (1906) who observed it
in the follicles of various reptiles, by Thing (1918) who.

noted its occurrence in turtles, and by Betz (1963) who described it in the water snake Natrix rhombifera. Boyd (1940) called this layer the striate zone in the gecko Hoplodactylus maculatus.

The zona pellucida of Sceloporus jarrovi is sur-rounded by several layers of granulosa cells (Figs. 3-5) consisting of small, intermediate and large types. The small (7 micra) and intermediate (11 micra) granulosa cells, which contain nuclei with a single nucleolus and non-vacuolated cytoplasm, are typically arranged in layers 1-3 cells thick along the zona pellucida and 1-2 layers thick along the connective tissue theca (Fig. 5). Between these areas are located 1-2 layers of large flask shaped granulosa cells (21 micra) (Fig. 4) which are called pyriform cells by Betz (1963). Each contains a large nucleolus (9 micra) with 1-2 densely staining nucleoli and a highly vacuolated cytoplasm. Some of the large granulosa cells communicate with the interior of the ovum through cytoplasmic extensions (Fig. 4) which are most frequently seen at the onset of yolk deposition in August.

Follicular wall connective tissue in S. jarrovi is organized into a thin theca interna (16 micra) consist-ing of connective tissue with flattened compressed nuclei and a thicker theca externa (32 micra) with round to poly-gonal shaped nuclei and moderate vascularization. The

amounts of intercellular fibrous tissue which are minimal in the theca interna become more abundant in the theca externa.

Atretic follicles are never abundant and are most frequently seen during the winter months at which time some of the non-ovulated follicles undergo degenerative changes. Corpora lutea are the most prominent elements in the ovary during the period from just after ovulation (November-December) until after parturition (June).

Reabsorption of ova from the oviduct appears to be uncommon in S. jarrovi. Only 6 out of 91 females (Table 7) showed evidence of this phenomenon by having fewer ova than corpora lutea and/or showing reabsorption in progress. It is noteworthy that all of these cases occurred late in the gestation period.

Ovarian Seasonal Cycle

September-November.--Yolk deposition (Fig. 5) takes place at increasingly rapid rates during this period and culminates with ovulation from mid-November to early December. There is a high positive correlation ($r = +.78$) between the variables snout-vent length and ovarian weight during the period of yolk deposition (Fig. 6, Table 8) as well as between snout-vent length and number of eggs in the oviduct ($r = +.89$) (Fig. 7, Appendix A). A sample of 85

Table 1. Ovary and body weights (gms), for ratios (% ovary wgt./body wgt.) in
Table 2, for <u>Sceloporus</u> <u>jarrovi</u>, April 1968-October 1969.

Month	N	Average Rgt. Ovary	Average Lft. Ovary	Total Average	Range	Average Body wgt.	Range
April	10	0.006	0.026	0.030	(0.006-0.204)	15.06	(7.96-29.23)
May	9	0.007	0.008	0.015	(0.006-0.026)	16.33	(9.23-28.69)
June	11	0.008	0.009	0.018	(0.008-0.024)	14.68	(8.52-23.10)
July	16	0.011	0.011	0.021	(0.007-0.042)	14.13	(10.16-20.31)
Aug.	10	0.015	0.017	0.032	(0.020-0.048)	15.43	(11.38-20.66)
Sept.	11	0.165	0.178	0.371	(0.070-0.993)	18.63	(12.31-24.08)
Oct.	16	0.606	0.570	1.176	(0.140-2.464	17.03	(8.39-25.89)
Nov.	12	0.565	0.485	1.050	(0.052-2.707)	15.78	(7.30-25.71)
Dec.	10	0.231	0.119	0.350	(0.032-0.996)	10.01	(5.67-15.08)

Table 1. (Continued)

Month	N	Average Rgt. Ovary	Average Lft. Ovary	Total Average	Range	Average Body wgt.	Range
Jan.	10	0.023	0.027	0.050	(0.022-0.062)	15.80	(9.19-21.46)
Feb.	13	0.018	0.017	0.036	(0.017-0.068)	14.06	(9.12-18.28)
March	11	0.022	0.020	0.043	(0.023-0.071)	16.98	(13.21-23.30)
April	15	0.013	0.013	0.026	(0.008-0.038)	16.64	(6.49-25.73)
May	15	0.007	0.008	0.015	(0.006-0.025)	17.07	(7.28-27.96)
June	13	0.006	0.006	0.012	(0.003-0.021)	15.59	(7.86-23.29)
July	12	0.007	0.008	0.015	(0.006-0.028)	12.61	(7.86-20.16)
Aug.	15	0.011	0.011	0.023	(0.011-0.054)	14.18	(7.35-24.71)
Sept.	13	0.029	0.029	0.058	(0.028-0.158)	14.87	(9.76-29.20)
Oct.	11	0.275	0.259	0.535	(0.132-0.923)	16.96	(14.08-21.22)

Table 2. Ratios (% ovary wgt./body wgt.) for Sceloporus
          jarrovi. (Data graphed in Fig. 1.)

Month	N	Ratio % Ovary wgt./ body wgt.	Range	95% Confidence Interval
April	10	0.094±0.007	(0.060-0.142)	0.078-0.110
May	9	0.095±0.011	(0.045-0.162)	0.070-0.120
June	11	0.112±0.015	(0.024-0.165)	0.079-0.145
July	16	0.150±0.013	(0.042-0.280)	0.123-0.177
Aug.	10	0.205±0.010	(0.132-0.233)	0.183-0.227
Sept.	11	1.753±0.436	(0.386-4.231)	0.781-2.724
Oct.	16	6.484±0.619	(1.666-10.496)	6.165-7.803
Nov.	12	8.870±1.932	(0.329-15.913)	4.618-13.120
Dec.	10	4.546±1.712	(0.322-13.404)	0.674-8.418
Jan.	10	0.312±0.014	(0.241-0.334)	0.281-0.343
Feb.	13	0.253±0.035	(0.181-0.390)	0.177-0.329
March	11	0.256±0.027	(0.159-0.436)	0.196-0.316
April	15	0.156±0.009	(0.100-0.211)	0.137-0.175
May	15	0.090±0.005	(0.052-0.114)	0.080-0.100
June	13	0.074±0.007	(0.019-0.108)	0.059-0.089
July	12	0.118±0.014	(0.082-0.226)	0.088-0.148
Aug.	15	0.170±0.012	(0.084-0.285)	0.143-0.196
Sept.	13	0.374±0.020	(0.262-0.543)	0.331-0.417
Oct.	11	3.020±0.377	(0.940-4.618)	2.179-3.860

Table 3. Monthly distribution of ovarian follicles (mm) for _Sceloporus jarrovi_.

Month	N	> 1 mm	1-2 mm	2-3 mm	3-4 mm	4-5 mm	5-6 mm	6-7 mm	7-8 mm	8-9 mm	9-10 mm
April	9	53(.90)	6(.10)	0	0	0	0	0	0	0	0
May	9	36(.80)	9(.20)	0	0	0	0	0	0	0	0
June	11	72(.89)	12(.11)	0	0	0	0	0	0	0	0
July	9	47(.57)	36(.43)	0	0	0	0	0	0	0	0
Aug.	8	40(.37)	65(.61)	1(.02)	0	0	0	0	0	0	0
Sept.	11	31(.18)	76(.46)	27(.16)	14(.08)	8(.04)	7(.04)	2(.01)	0	0	0
Oct.	12	51(.36)	33(.23)	2(.01)	1(.00)	0	8(.05)	23(.16)	20(.14)	1(.00)	0
Nov.	12	21(.36)	11(.18)	0	0	0	0	2(.03)	5(.08)	17(.29)	2(.03)
Dec.	11	36(.64)	14(.25)	0	2(.03)	0	0	0	1(.01)	3(.05)	0
Jan.	10	25(.53)	20(.42)	1(.02)	1(.02)	0	0	0	0	0	0
Feb.	12	63(.79)	17(.21)	0	0	0	0	0	0	0	0
March	10	43(.83)	9(.17)	0	0	0	0	0	0	0	0
April	11	48(.84)	9(.16)	0	0	0	0	0	0	0	0
May	12	61(.94)	4(.06)	0	0	0	0	0	0	0	0
June	11	58(.93)	4(.07)	0	0	0	0	0	0	0	0
July	10	27(.25)	80(.75)	0	0	0	0	0	0	0	0
Aug.	11	79(.57)	60(.43)	0	0	0	0	0	0	0	0
Sept.	10	37(.25)	74(.62)	28(.13)	0	0	0	0	0	0	0
Oct.	11	52(.30)	61(.35)	14(.08)	9(.06)	16(.10)	16(.10)	3(.01)	0	0	0

Table 4. Monthly means for numbers of ovarian follicles
          for _Sceloporus_ _jarrovi_. (Summary of data from
          Table 3.)

Month	N	Mean	Range	95% Confidence Interval
April	9	6.55±0.686	3-11	4.97- 8.13
May	9	5.11±0.351	4-7	4.31- 5.91
June	11	8.12±0.523	6-12	6.96- 9.28
July	9	9.22±0.741	7-12	7.52-10.92
Aug.	8	13.25±1.176	8-18	10.47-16.03
Sept.	11	15.18±1.163	9-23	12.59-17.77
Oct.	12	11.58±0.701	8-16	10.04-13.12
Nov.	12	4.83±1.364	0-12	1.83- 7.83
Dec.	11	5.81±0.711	3-10	4.23- 7.39
Jan.	10	4.80±0.785	1-8	3.03- 6.57
Feb.	12	6.66±0.512	2-11	5.54- 7.78
March	10	5.20±0.592	3-9	3.89- 6.51
April	11	5.18±0.601	3-8	3.85- 6.51
May	12	5.41±0.500	3-8	4.31- 6.51
June	11	5.63±0.719	3-9	4.03- 7.23
July	10	10.70±0.920	7-15	8.62-12.78
Aug.	11	12.63±0.694	10-17	11.09-14.17
Sept.	10	13.90±0.433	11-26	12.93-14.87
Oct.	11	15.54±1.281	9-22	12.69-18.39

Table 5. Monthly size distribution of corpora lutea (maximum diameters, mm) in
          Sceloporus _jarrovi_, April 1968-June 1968, November 1968-June 1969.

Month	N	Corpora Lutea (Number)	0-1	1-2	2-3	3-4	4-5
April	9	27	0	27(1.00)	0	0	0
May	9	29	0	29(1.00)	0	0	0
June	11	30	1(.02)	28(.96)	1(.02)	0	0
Nov.	5	17	0	0	0	9(.53)	8(.47)
Dec.	7	15	0	0	2(.13)	10(.67)	3(.20)
Jan.	10	40	0	0	26(.65)	14(.35)	0
Feb.	12	42	0	2(.05)	36(.85)	4(.10)	0
March	10	36	0	8(.22)	24(.67)	4(.11)	0
April	11	46	0	39(.88)	7(.12)	0	0
May	12	43	0	43(1.00)	0	0	0
June	11	28	0	28(1.00)	0	0	0

Table 6. Mean monthly variation of corpora lutea (maximum
          diameters, mm) in Sceloporus jarrovi for periods
          April 1968-June 1968, November 1968-June 1969.

Month	N	Corpora Lutea	Mean Length	95% Confidence Interval
April	9	27	1.41±0.004	1.41-1.41
May	9	29	1.38±0.104	1.14-1.62
June	11	30	1.45±0.147	1.12-1.78
Nov.	5	17	3.86±0.122	3.52-4.20
Dec.	7	15	3.35±0.175	2.92-3.78
Jan.	10	40	2.80±0.129	2.51-3.09
Feb.	12	42	2.47±0.080	2.29-2.65
March	10	36	2.24±0.136	1.94-2.54
April	11	46	1.62±0.067	1.47-1.77
May	12	43	1.29±0.022	1.25-1.33
June	11	28	1.33±0.069	1.18-1.48

Table 7. Monthly incidence of ova reabsorption in
Sceloporus jarrovi, November 1968-June 1969.
(Raw data in Appendix A.)

Month	N	Reabsorption	No Reabsorption
Nov.	5	0	5
Dec.	8	0	8
Jan.	10	0	10
Feb.	13	0	13
March	11	0	11
April	15	1	14
May	16	1	15
June	13	4	9
NO.	91	6	85
		(7%)	(93%)
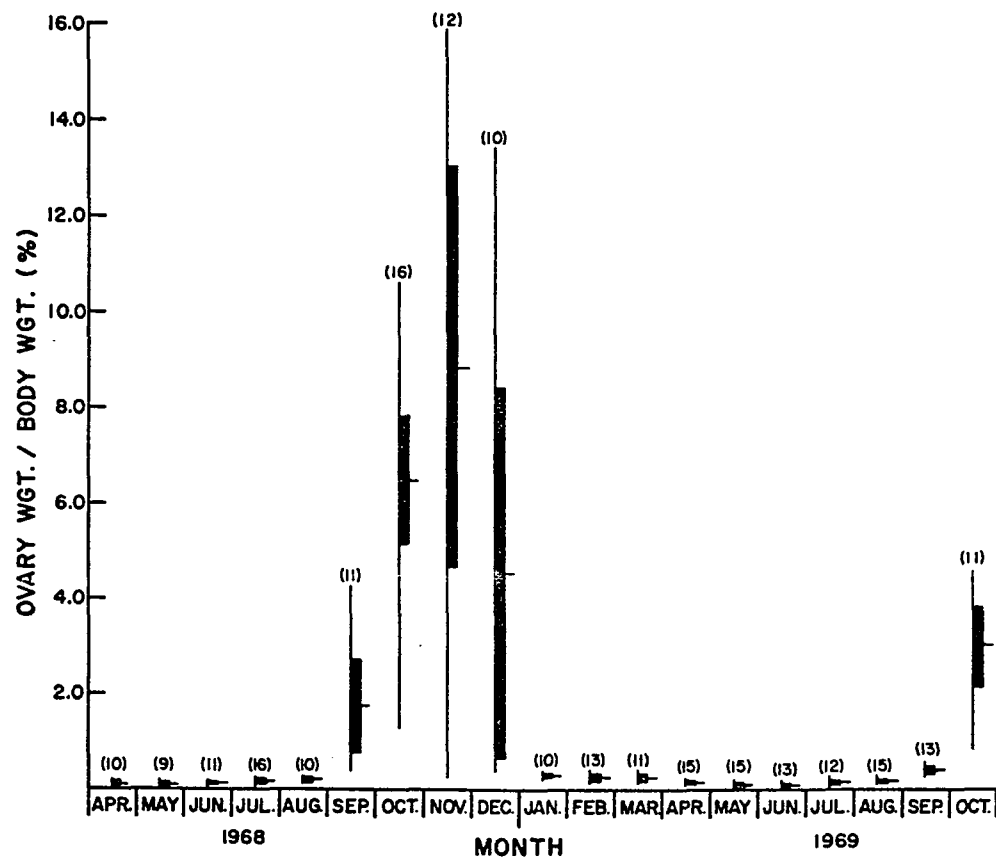
Fig. 1. Modified Dice-Lerras graph showing seasonal changes in % ovary
        wgt./body wgt. for <u>Sceloporus</u> <u>jarrovi</u>, April 1968-October 1969.
        (Data from Table 2. Bars represent 95% confidence intervals.)
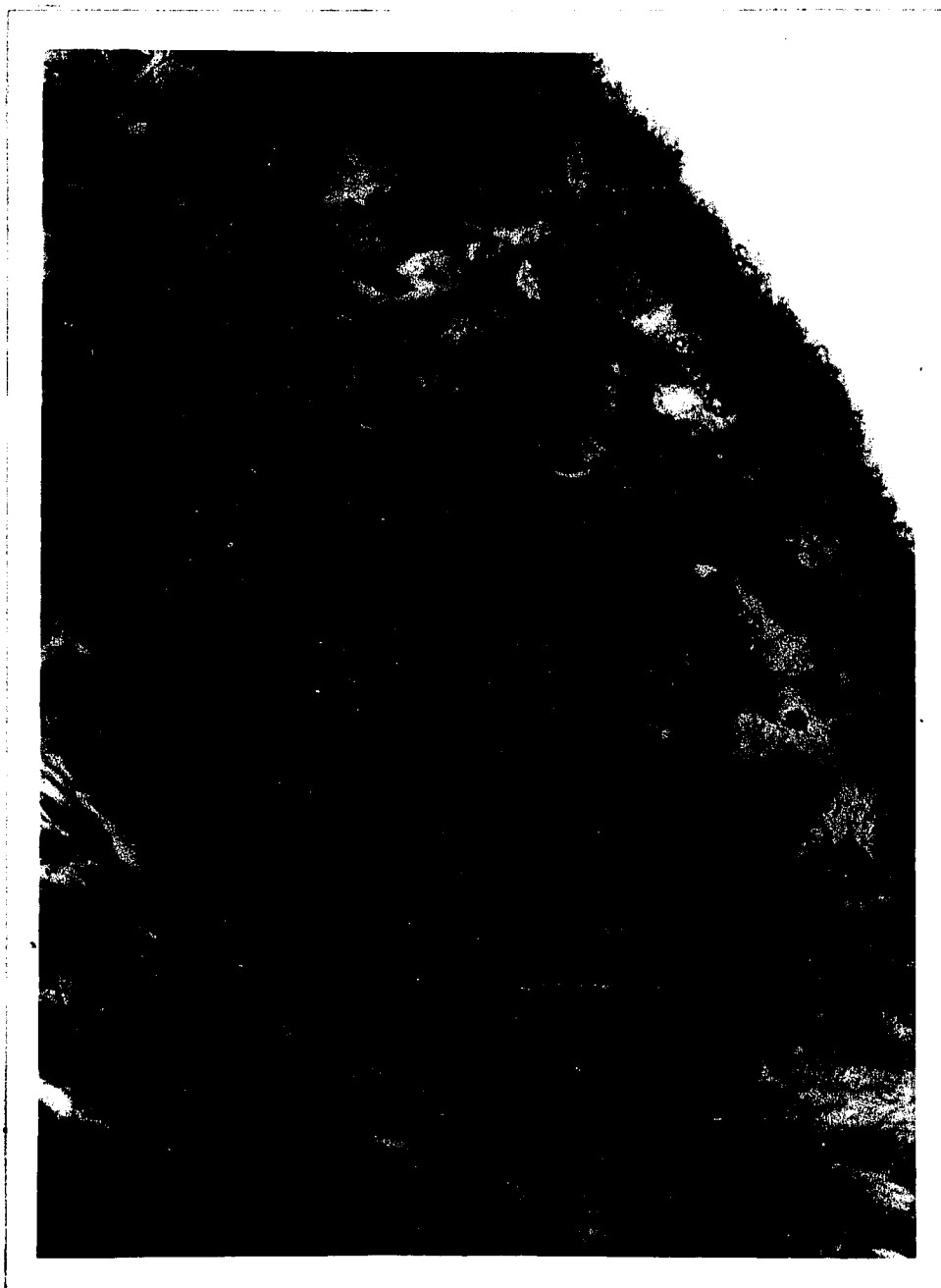
Fig. 2. Germinal epithelium from ovary of Sceloporus
         jarrovi, July 10, 1965. (Note abundant oocytes
         (arrow), 760X.)

Fig. 3. Zona pellucida from follicle of _Sceloporus jarrovi_
ovary. (Note zona radiata (A) and outer layer
(B), 1920X.)

Fig. 4. Granulosa from <u>Sceloporus jarrovi</u> ovary, August
1966. (Note discharging pyriform cell (arrow),
1920X.)
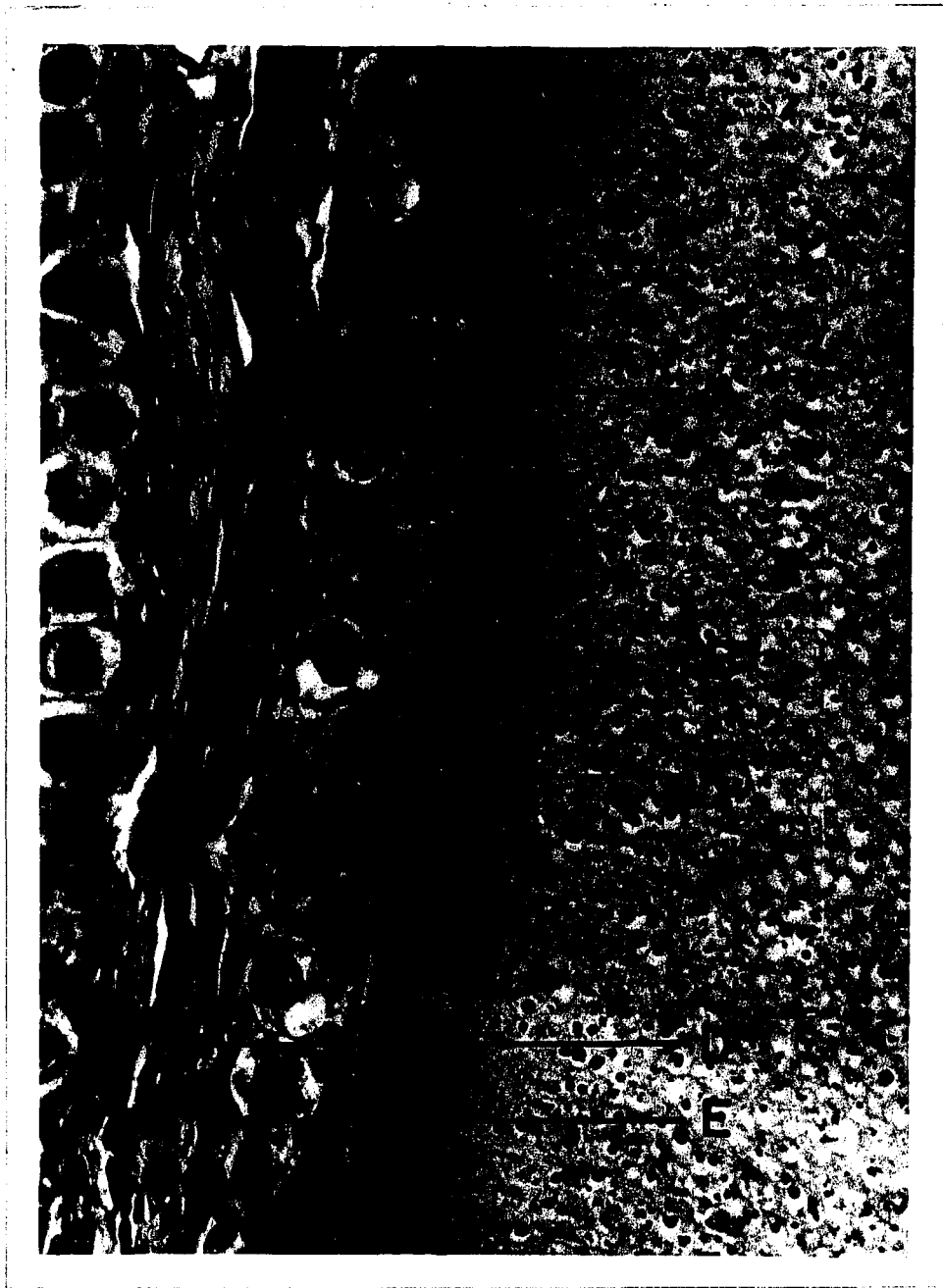
Fig. 5.   Early yolk deposition in ovary of Sceloporus
          jarrovi, September 9, 1965. (Note uneven dis-
          tribution of yolk granules with largest concen-
          trations on periphery of follicle, A, zona
          pellucida, B, pyriform cell, C, granulosa cell,
          D, theca externa, E, theca interna, 300X.)

females had a weighted mean of 6.77 eggs for both oviducts
(Table 9). By the end of vitellogenesis the mature egg
is between 8 and 9 mm in diameter and the follicular epi-
thelium is reduced to a single layer of small cells.

Ovulation occurs when the follicular epithelium
bursts and the ovum is expelled into the body cavity. The
surface of the ovum is highly adhesive which may facilitate
its entrance into the oviduct. Trans-ovarian migration of
ova (from one oviduct to the other) is relatively common
and occurs as much as 42% of the time (Table 10); migra-
tions will not be detected if the number of eggs and corpora
lutea on each side are equal. An examination of 26 eggs
from eight females collected during November-December 1968
revealed that all contained blastoderms indicating fertili-
zation had occurred (Fig. 8), presumably soon after ovula-
tion.

The wall of a ruptured follicle appeared translucent
when observed moments after ovulation. Its sides were
raised and there was a blood-stained depression in the
crater-like cavity marking the site of ovulation. Lumina
of freshly ovulated follicles are approximately 4 mm in
diameter. Sections revealed that the granulosa cells of the
collapsed follicle undergo a rapid hypertrophy immediately
after ovulation and produce masses of large luteal cells
that soon fill the old follicular cavity. The luteal cell

mass is completely surrounded by a moderately vascularized theca externa characterized by massed collagenous fibers with scattered fibroblasts and a much thinner theca interna containing few fibers and many fibroblasts. Granulosa cells are seen digesting patches of remaining yolk. No follicular stresia was observed during this period.

Luteal cells contain round to oblong shaped nuclei (Fig. 9) with one nucleolus. The cytoplasm is lightly granulated and highly vacuolated. Invasion of the corpus luteum by fibroblasts or capillaries does not occur although moderate amounts of small blood vessels may be seen in the surrounding thecae. The corpora lutea are largest at their time of formation (November-December) and undergo a slow but progressive decrease in size (Tables 5-6) up until the time of parturition (June) after which a rapid and final involution occurs.

December-March.--The ovaries have their simplest organization during the winter post-ovulatory period consisting of several large secretory corpora lutea and from 4-5 small (less than 2 mm) follicles (Tables 3-4). Interstitial tissue is present in reduced amounts throughout this period. The central ooplasm of the winter follicles is opaque except for some vacuolization in the center. Vacuoles are common in the pyriform cell cytoplasm but are smaller and less abundant in comparison to their frequency

in late summer, just prior to and during early yolk deposition.

Follicles exhibit no growth during this period and many of them undergo gradual atresia. The early stages of follicular atresia (Fig. 10) are seen as a slightly vacuolated ooplasm, a gradual disappearance of the vitelline membrane, zona pellucida, zona radiata and an increase in the number of granulosa cells. The ooplasm pulls away from the granulosa in certain areas of the follicle. Mitotic figures are common among the granulosa cells.

In later stages of atresia the follicle takes on a shrunken, wrinkled appearance. The larger proximal granulosa cells become filled with large vacuoles into which the ooplasm appears to be diffusing and polymorphonuclear leucocytes are scattered about in the remaining ooplasm (Fig. 11). Granulosa cells do not migrate into the follicle until atresia is almost completed, at which time they follow the edges of the erroding yolk mass toward the center of the follicle.

In larger follicles, including those which underwent vitellogenesis but did not ovulate, clusters of granulosa cells may hypertrophy and become "giant cells" similar to those described by Boyd (1940) in Hoplodactylus maculatus and Altland (1951) in Terrapene ornata (Fig. 12). These frequently occur in groups which extend for varying lengths

into the follicular cavity with greatly enlarged giant cells located at the distal tips. Presumably these extensions permit a greater granulosa surface to be exposed to the ooplasm, thereby allowing for more rapid yolk digestion.

Atresia is completed with the disappearance of the ooplasm. The center of the follicle (Fig. 13) is a mixture of connective tissue, hypertrophic granulosa cells, leucocytes, globules of unphagocytized ooplasm and fibroblasts.

As few atretic follicles are seen in ovaries taken from females during the spring, follicular atresia is apparently completed in most cases within the span of three months (December-February).

April-mid-June.--There is a slight decrease in ovarian mass (Tables 1-2) due to the shrinkage of the corpora lutea from oblong convoluted bodies as seen during the winter to smaller circular or rectangular ones (Tables 5-6). In some cases the theca interna may be absent and the theca externa is usually greatly reduced. Concomitant luteal cell depletion is indicated by sickle or crescent shaped nuclei (Fig. 14). The cytoplasm contains one large vacuole rather than the scattering of small ones seen in luteal cells just after ovulation (Fig. 9). Secretions have presumably diminished as a result of this decrease in

cytoplasmic volume. Atretic follicles become progressively less common during the spring months.

Mid-June-August.--Changes occurring in the ovary during this period include growth among the follicles and a degeneration and destruction of the corpora lutea, commencing immediately after parturition in mid-June. No cases of follicular atresia were noted during this period.

The corpora lutea have shrunk to their smallest size in mid-June (Tables 5-6) at a time roughly seven months after ovulation. Their final destruction begins approximately five days after mid-June parturition with the appearance of large vacuoles that are first observed in the center of the corpus luteum and then spread progressively outward. By 15 days after parturition (Fig. 15) the nuclei of the luteal cells are irregularly shaped and the broken cell walls form a fibrous network. The theca interna has disappeared and the theca externa continues to show reduction.

Corpus luteum destruction is essentially completed by 30-40 days after parturition. The numbers of luteal cell nuclei have been drastically reduced, cell boundaries are almost totally indistinguishable and the center of the degenerating gland resembles a reticular network. Many of the remaining capillaries in the theca have disintegrated, leaving a heterogeneous mixture of broken red blood cells.

The theca externa undergoes further reduction and is in-
filtrated by luteal cell nuclei; vacuoles are abundant and
no capillaries are seen.

Remanents of the corpora lutea (Fig. 16) (homolog-
ous to mammalian corpora albicans) may be seen microscop-
ically as late as 70 days after parturition at which time
some of the luteal cell nuclei remain interspersed in a
matrix of fibrous connective tissue.

After parturition there is an increase in the size
of the follicles which have remained largely inactive dur-
ing the winter months (Tables 3-4). These follicles, 1-2
mm in size, which number from 3-4, begin to accumulate yolk
in late August, and ovulation follows in late November or
early December. Ooplasm in the center of the follicles is
relatively homogeneous in contrast to the central vacuoliza-
tion frequently observed in winter follicles.

A proliferation of oocytes occurs in the germinal
epithelium beginning in early July and occurs conspicuously
for six to eight weeks (Fig. 2). Each primary follicle
within the germinal bed consists of a large central oocyte
which is completely surrounded by a single layer of follicle
cells that will eventually become the granulosa. The
nuclei of the primary oocytes are oval and contain one
nucleolus.

By late August yolk deposition is underway in follicles 1.5 mm in diameter or larger with the appearance of densely staining deuteroplasmic granules (Fig. 5). These first appear enclosed in ooplasmic vacuoles on the periphery of the follicle and gradually spread throughout.

It is noteworthy that yolk deposition (Fig. 1, Tables 1-3) barely begun in September 1969 was well advanced on the same date of the previous year.

Discussion

Previous workers including Boyd (1940), Samuel (1944), Bragdon (1952), and Betz (1963) have suggested that intermediate and large granulosa cells arise separately by differentiation, i.e., from small granulosa cells. As the cytological features of all three cell types are similar, it is obviously conceivable that they may represent a developmental series and instead of intermediate and large granulosa cells developing from different small granulosa cells, development may proceed in a direct sequence, from small through intermediate to large granulosa cells. The present investigation has not produced evidence for either of these alternatives.

Betz (1963) has suggested that since the large granulosa (pyriform) cells of Natrix rhombifera discharge their contents into the ooplasm of developing follicles,

Table 8. Data for regression of ovarian weight (gms) on snout-vent length (mm) for 16 *Sceloporus jarrovi* females, October 1968.

Number	Snout-vent Length (X)	Ovarian Weight (Y)	r	P	Regression Equation
1	60.0	0.139	+.782	<.001	$Y = -3.81 + .067(X)$
2	64.0	0.599			
3	71.0	0.499			
4	74.0	0.906			
5	74.0	1.063			
6	75.0	0.825			
7	76.0	1.121			
8	76.0	1.644			
9	77.0	0.699			
10	80.0	1.829			
11	81.0	0.875			
12	82.0	1.239			
13	82.0	1.159			

Table 8. (Continued)

Number	Snout-vent Length (X)	Ovarian Weight (Y)	r	P	Regression Equation
14	83.0	2.159			
15	84.0	1.613			
16	86.0	2.464			

Table 9. Means and ranges for distribution of ova in oviducts of Sceloporus jarrovi, November 1968-June 1969. (Weighted mean for all data (N=85) is 6.77. Raw data in Appendix A.)

Month	N	Ova in Right Oviduct	Range	Ova in Left Oviduct	Range	Total in Both Oviducts	Range	95% Confidence Interval	Average Ova per Female Weighted Mean
Nov.	5	3.6	3-6	3.8	2-4	7.4	6-9		6.77 (N=85)
Dec.	8	3.1	2-5	3.0	2-5	6.1±0.79	4-10	4.25-7.99	
Jan.	10	3.9	2-6	3.4	2-5	7.3±0.58	4-11	5.97-8.63	
Feb.	13	3.4	1-6	3.1	1-5	6.5±0.66	2-10	5.02-7.90	
March	11	3.8	3-6	3.7	3-5	7.5±0.42	6-10	6.62-8.46	
April	14	3.8	1-8	3.4	1-6	7.3±0.79	2-12	5.56-8.96	
May	15	3.7	2-5	2.8	1-5	6.5±0.60	3-10	5.25-7.81	
June	9	3.1	1-4	2.4	1-4	5.6±0.73	3-9	3.87-7.23	

Table 10. Extra-uterine migration of ova in _Sceloporus jarrovi_. (Raw data in Appendix B.)

Month	N	Extra-uterine Migration of Ova	No Extra-uterine Migration of Ova
Nov.	5	1	4
Dec.	8	3	5
Jan.	10	6	4
Feb.	13	4	9
March	11	3	8
April	14	9	5
May	15	8	7
June	9	2	7
NO.	85	36	49
		(42%)	(58%)
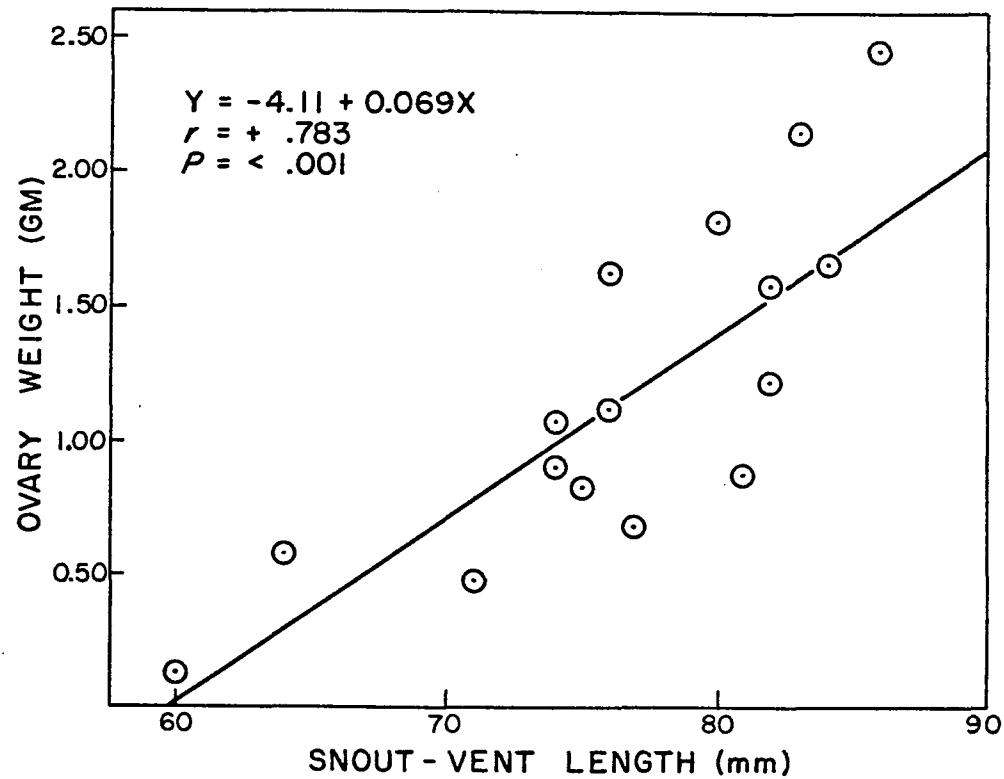
Fig. 6.   Regression of ovarian weight (gms) on snout-vent length (mm) for 16
Sceloporus jarrovi females, October 1968.   (Data from Table 8.)
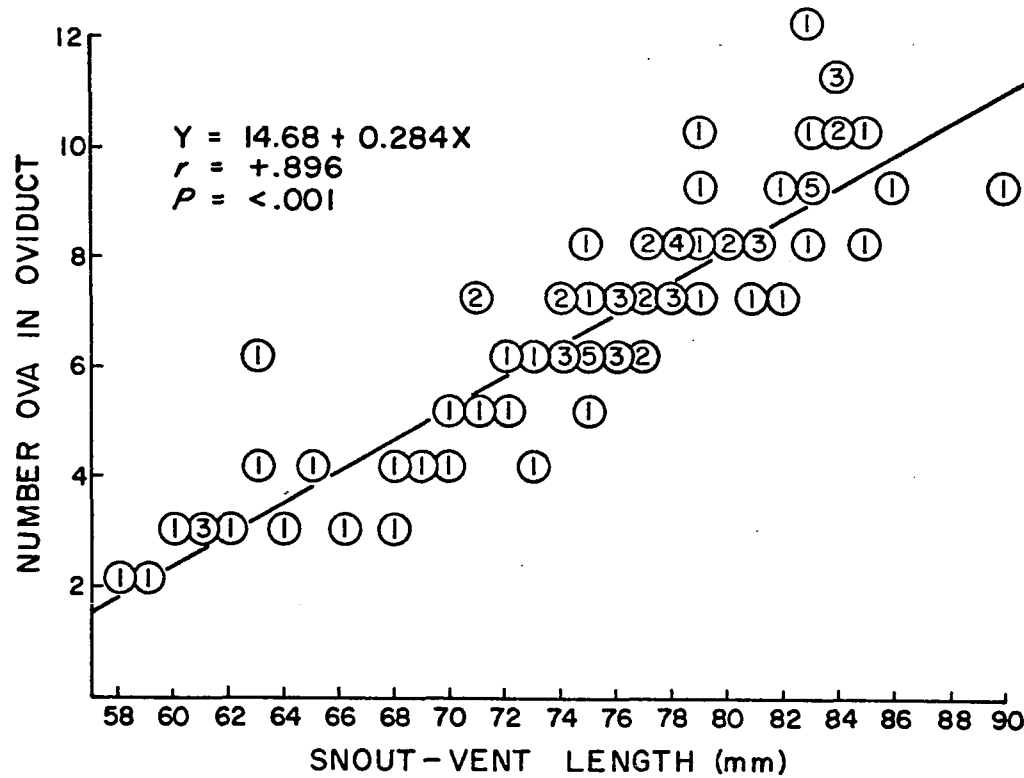
Fig. 7. Regression of number of ova on snout-vent length for 85 Sceloporus jarrovi females. (Circled numbers represent frequency of females. Data in Appendix B.)
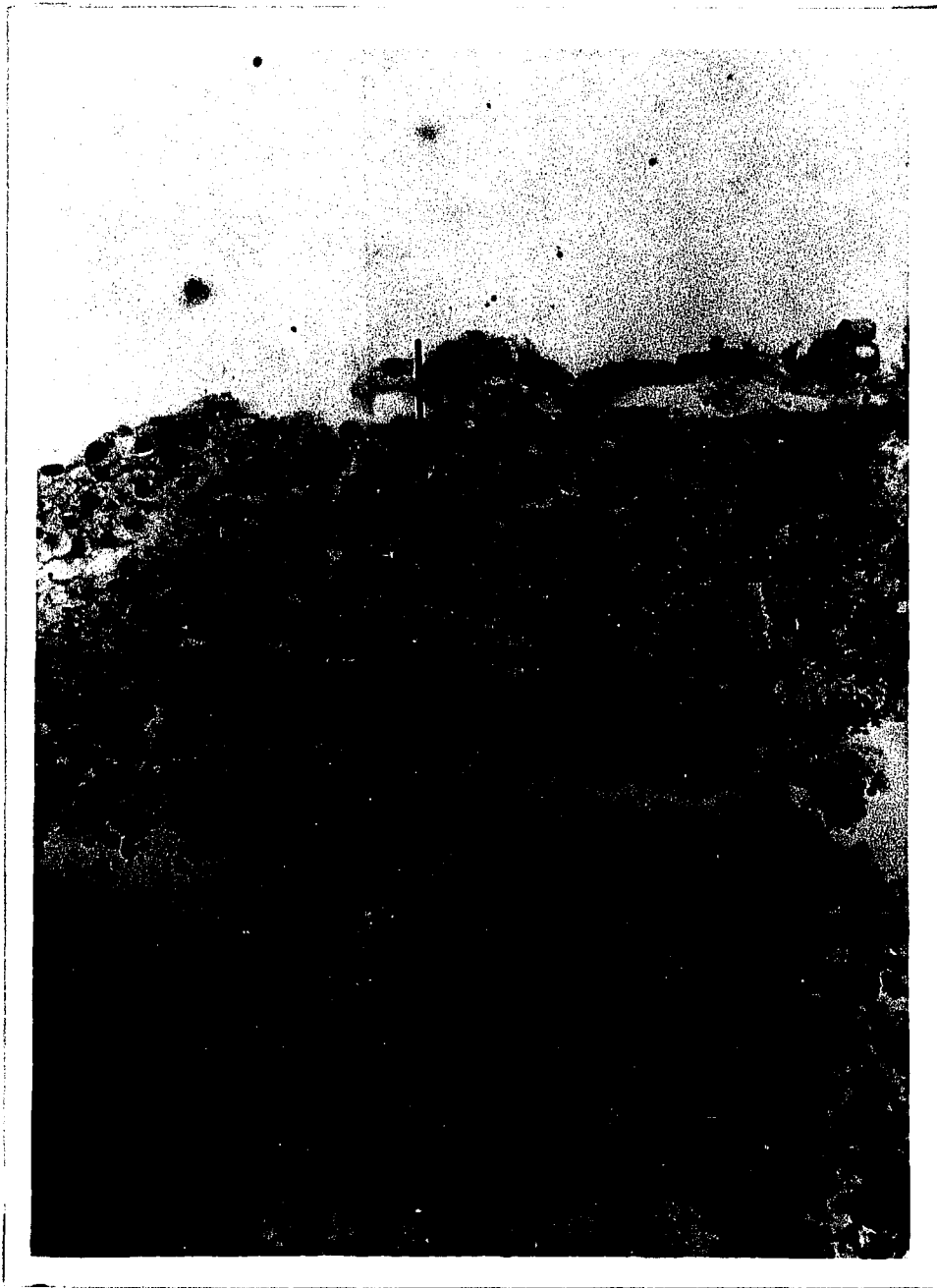
Fig. 8. Portion of blastoderm disc (arrow) from female
of <u>Sceloporus</u> <u>jarrovi</u>, January 6, 1969. (300X)
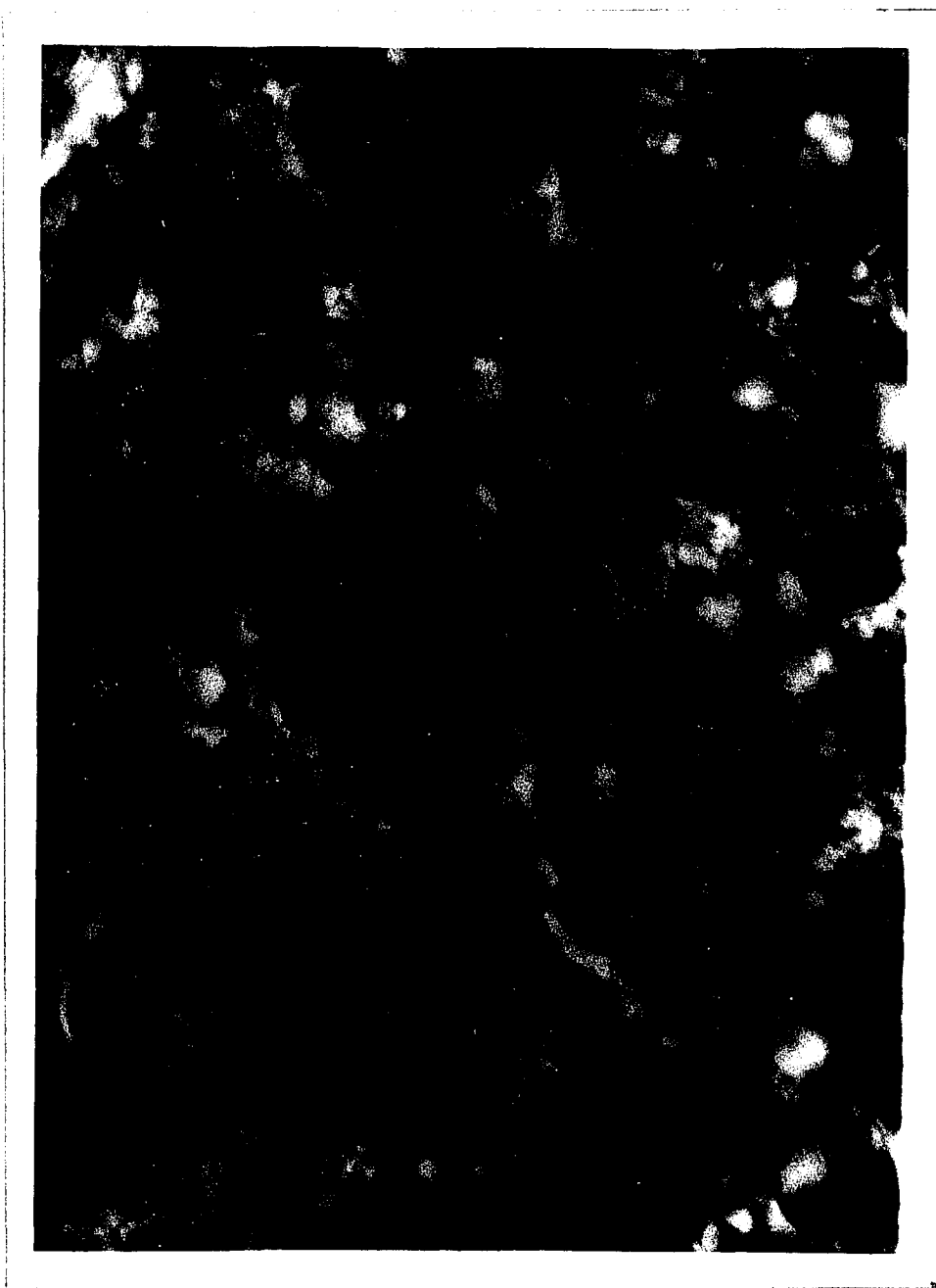
Fig. 9. Secretory corpus luteum from ovary of Sceloporus jarrovi, December 10, 1967. (Note large luteal cell nuclei, 1920X.)

Fig. 10. Early follicular atresia in ovary of <u>Sceloporus</u>
<u>jarrovi</u>, January 14, 1967. (Note disappearance
of zona pellucida and proliferation of granulosa
cells (arrow), 760X.)
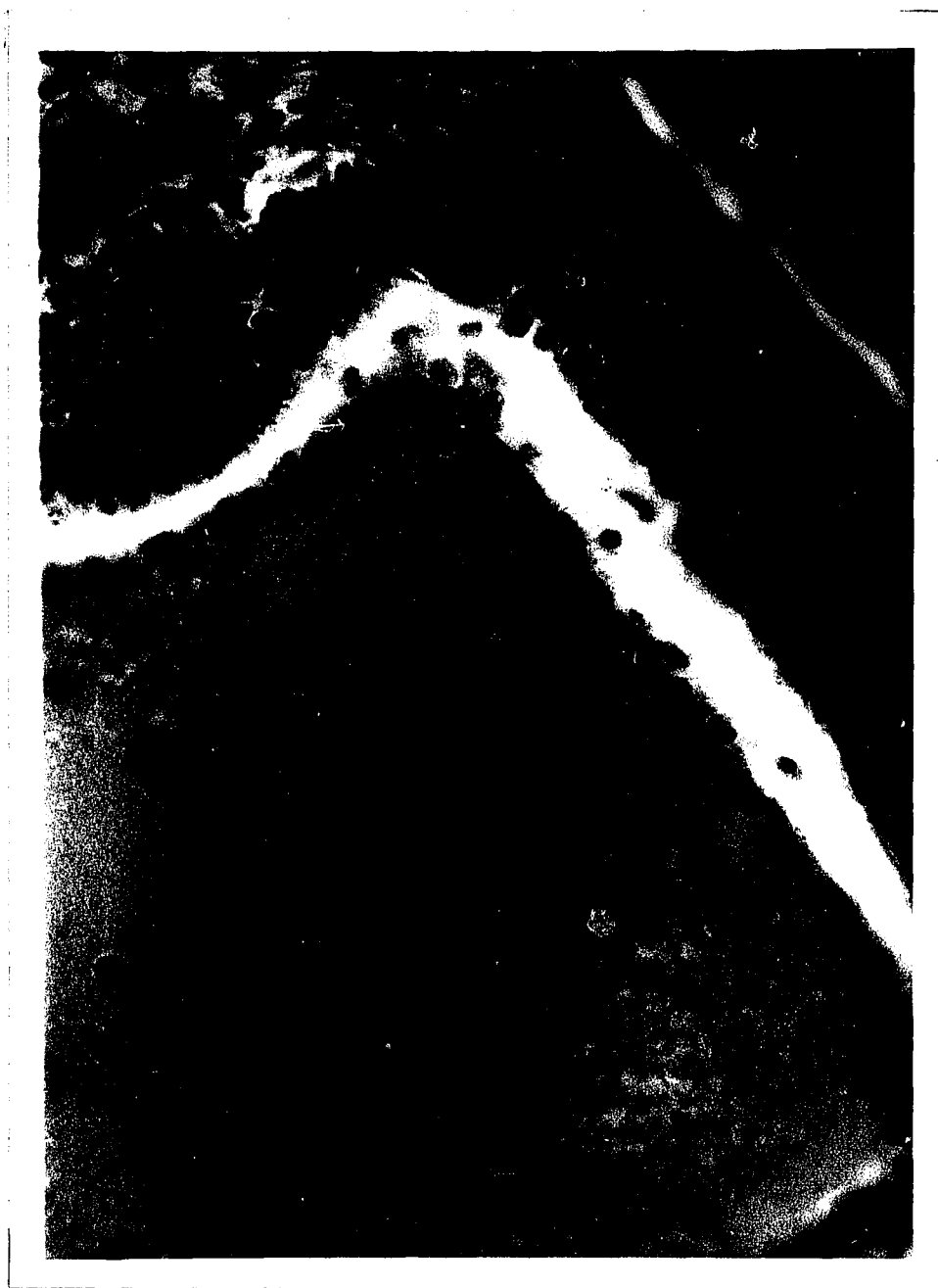
Fig. 11.   Follicular atresia in ovary of <u>Sceloporus jarrovi</u>,
          March 21, 1965. (Note invasion of leucocytes
          into ooplasm, 300X.)
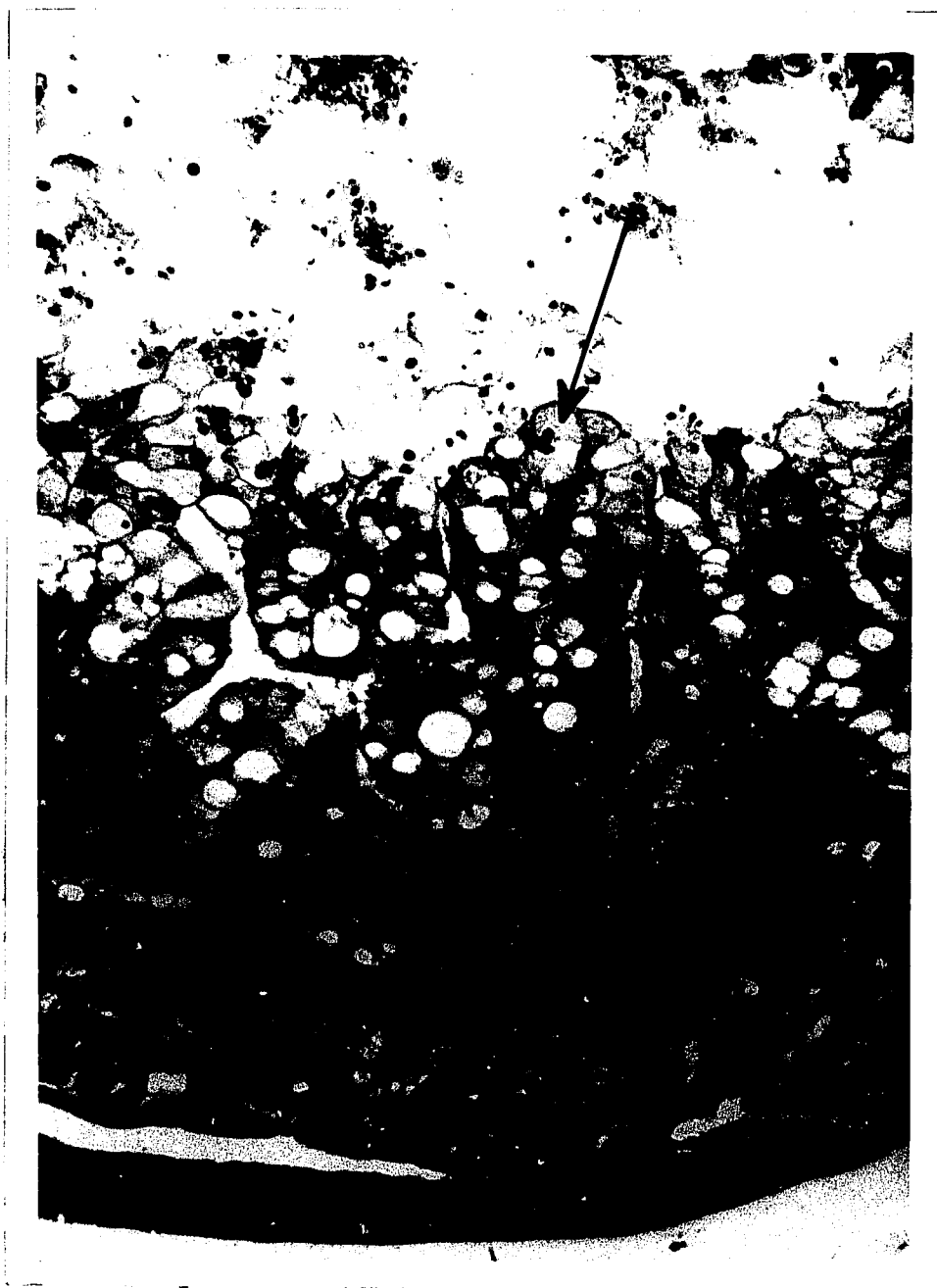
Fig. 12. Follicular atresia in ovary of _Sceloporus jarrovi_,
          November 10, 1968. (Hypertrophied granulosal
          cells (giant cells) extend into follicular lumen
          (arrow), 120X.)

Fig. 13.   Late follicular atresia in ovary of <u>Sceloporus</u>
           <u>jarrovi</u>, February 10, 1967.   (Note leucocyte
           (arrow) in ooplasm remanent, 300X.)
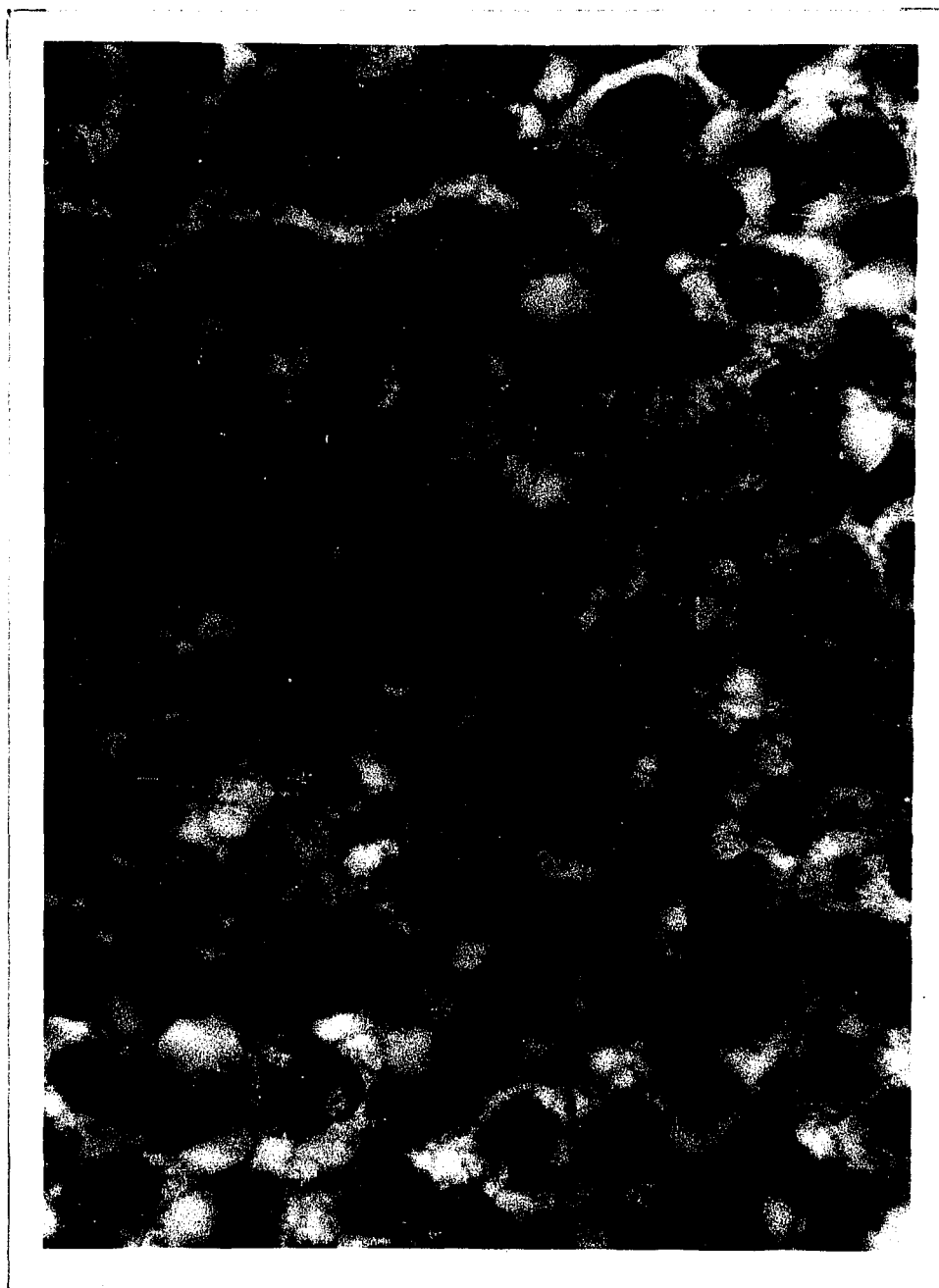
Fig. 14. Depleted corpus luteum from ovary of Sceloporus
          jarrovi, May 19, 1967. (Note irregularly shaped
          nuclei, 1920X.)

Fig. 15. Regressing corpus luteum from ovary of Sceloporus
jarrovi, June 25, 1966. (Note irregularly shaped
luteal cell nuclei and fibrous tissue network
(arrow), 300X.)

Fig. 16. Remanent of corpus luteum (corpus albicans) from
ovary of Sceloporus jarrovi, August 30, 1965.
(Corpus luteum has been largely replaced by con-
nective tissue (arrow) approximately 10 weeks
after parturition, 300X.)

their secretions may in some way furnish precursors of the deuteroplasmic granules. Observations made on Sceloporus jarrovi ovaries lend support to this theory. Although discharging pyriform cells may be found throughout the year, they are clearly most abundant during the periods just prior to and during yolk deposition (August-September). Thus, the granulosa cells of Sceloporus jarrovi already vitally involved in two ovarian processes (follicular atresia and luteal tissue formation) may play a role in a third, yolk deposition.

The process of follicular atresia in Sceloporus jarrovi appears to be similar to that reported for other reptiles (Boyd 1940, Miller 1948, and Bragdon 1952) in that granulosa cells play a major role in phagocytizing of yolk granules and removal of follicular debris.

There are conflicting reports on the frequency of follicular atresia among different lizards. Boyd (1940) reports that it is a rarity in the gecko Hoplodactylus maculatus.. Bragdon (1952) felt it was not an uncommon occurrence in the garter snake Thamnophis sirtalis and the water snake Natrix sipedon. Miller (1948), working with Xantusia vigilis, found that 20 to 40 follicles begin development every year but all but one or two undergo atresia so that there is at least one atretic follicle in every ovary at any given time. Betz (1963) reported that atresia

may occur in the follicles of the water snake <u>Natrix</u>
<u>rhombifera</u> at any stage of development but is more fre-
quently seen in follicles with a polymorphic granulosa,
or in mature follicles which have not ovulated. Follicular
atresia is fairly common in <u>Sceloporus jarrovi</u> during the
winter months but is essentially absent during the period
from late spring to early fall.

Corpus luteum formation in <u>Sceloporus jarrovi</u>
resembles that of other reptiles (Rahn 1938) in that the
granulosa cells of the collapsed follicle, which appear
to be solely responsible for formation of luteal cells,
hypertrophy, fill the old follicular cavity immediately
after ovulation and are transformed into luteal tissue.

Varying amounts of fibroblasts and capillaries
invade the corpora lutea of different lizards. Essentially
no invasion occurs in <u>Sceloporus jarrovi</u> and the viviparous
skinks <u>Lygosoma</u> (<u>Hinulia</u>) <u>quoyi</u>, <u>L.</u> (<u>Hemiergis</u>) <u>quadri-</u>
<u>digitatum</u> and <u>Egernia whitei</u> (Weekes 1934). In <u>Xantusia</u>
<u>vigilis</u> (Miller 1948) and <u>Hoplodactylus maculatus</u> (Boyd
1940) moderate amounts of fibroblasts, but no capillaries,
penetrate. Both fibroblasts and blood vessels are present
in the luteal cell mass of the viviparous <u>Lacerta vivipara</u>,
<u>Lygosoma</u> (<u>L.</u>) <u>weeksae</u> and <u>Lygosoma</u> (<u>L.</u>) <u>entrecasteauxi</u>
(Weekes 1934). In <u>L.</u> <u>vivipara</u> the fibroblasts penetrate
individual luteal cells while in <u>L.</u> (<u>L.</u>) <u>weeksae</u> and <u>L.</u>

(L.) entrecasteauxi the fibroblasts are associated with the blood vessels and no inter-luteal cell penetration occurs.

The presence of corpora lutea has been reported in both oviparous and viviparous forms (Table 11). I have confirmed their presence in the following additional species: Holbrookia maculata, Phrynosoma cornutum, P. douglassi and P. solare.

Duration of corpora lutea in lizards appears to be in most cases for as long as the egg (oviparous forms) or embryo (viviparous forms) remains within the oviduct. Corpora lutea degenerate soon after egg laying in oviparous forms while in viviparous forms corpora lutea do not usually totally regress until after parturition although varying amounts of degeneration occur by the terminal stages of gestation (as noted for Sceloporus jarrovi and others, Table 9).

Exceptions involving shorter existences may be found in the following two cases. Degeneration of the corpora lutea is completed by the time of egg laying in the oviparous Amphiboluris muricatus (Weekes 1934) and luteal regression begins before the completion of the gestational period in the viviparous Hoplodactylus maculatus (Boyd 1940). A possible exception for longevity may be found in Holbrookia texana; Johnson (1960) reported that corpora lutea from early spring were still evident at the

Table 11. Reports on longevity of corpora lutea in various lizards.

Species	Duration	Report
	OVIPAROUS SPECIES	
Gekkonidae		
Amphibolurus muricatus	Regression completed by egg laying	Weekes (1934)
Leiolopisma rhomboidalis	Regress shortly after egg laying	Wilhoft (1963)
Iguanidae		
Holbrookia texana	Regression during winter	Johnson (1960)
Sceloporus orcutti	Regress shortly after egg laying	Mayhew (1963)
Uma inornata	Regress shortly after egg laying	Mayhew (1965)
Uma notata	Regress shortly after egg laying	Mayhew (1966a)
Uma scoparia	Regress shortly after egg laying	Mayhew (1966b)
Teiidae		
Cnemidophorus hyperythrus beldingi	Regress shortly after egg laying	Bostic (1966)
Cnemidophorus sexlineatus	Regress shortly after egg laying	Hoddenbach (1966)
Cnemidophorus tigris	Regress shortly after egg laying	McCoy (1965)

Table 11. (Continued)

Species	Duration	Report
	VIVIPAROUS SPECIES	
Gekkonidae		
Hoplodactylus maculatus	Pronounced regression by parturition	Boyd (1940)
Lygosoma (L.) entrecasteauxi	Pronounced regression by parturition	Weekes (1934)
Lygosoma (Hinulia) quoyi	Pronounced regression by parturition	Weekes (1934)
Lygosoma (L.) quoyi	Pronounced regression by parturition	Weekes (1934)
Iquanidae		
Sceloporus cyanogenys	Maintained throughout most of gestation period	Crisp (1964)
Sceloporus jarrovi	Moderate regression by parturition	Goldberg (1970)
Lacertidae		
Lacerta vivipara	Pronounced regression by parturition	Weekes (1934)
Xantusidae		
Xantusia vigilis	Pronounced regression by parturition	Miller (1948)

time the lizards entered hibernation. Unfortunately he

failed to confirm these observations histologically and

his claims have been questioned by Tinkle (1967).

The report by Cunningham and Smart (1934) that the

ruptured follicle of oviparous forms undergoes immediate

reduction and absorption can be questioned in view of their

obvious errors in interpreting ovarian structures. They

claim that few changes have occurred in a ruptured follicle

from Lacerta viridis which has already transformed into a

corpus luteum; their photomicrograph of a supposedly de-

generating post-ovulatory follicle is clearly an atretic

follicle that did not ovulate. This matter is discussed

in detail in Boyd (1940).

The precise role played by the corpus luteum has

not been determined to date for reptiles. Bragdon (1951)

reported that young continued to develop in female

Thamnophis sirtalis and Natrix sipedon that were ovari-

ectomized in the middle third of pregnancy. He concluded

that the presence of functional corpora lutea was not

necessary for development of young.

Since the corpora lutea of Sceloporus jarrovi

undergo a progressive size decrease throughout the winter

(Tables 5-6), with cytoplasmic depletion becoming evident

late (April-June) in the gestation period, it is plausible

that their secretions play some role during the intra-
uterine development of the young.

A noticeable and significant (P<.01) yearly varia-
tion in the rate of yolk deposition occurs in Sceloporus
jarrovi (Fig. 1) and has also been reported in Uta
stansburiana by Tinkle (1961). It is presumably influenced
by the same factors (rainfall and insect populations) that
affect the number of seasonal clutches of oviparous lizards
(Mayhew 1965, 1966a, b).

THE OVIDUCTS

Gross Morphology

The oviducts of Sceloporus jarrovi are paired
structures that are suspended from the dorsal body wall
by mesenteries and may be divided into an anterior in-
fundibulum, a middle uterus and a posterior vagina. Their
morphology is variable depending on the season of the year
in which they are examined.

During the months in which they do not contain ova
(January-October), they are highly convoluted, compressed,
whitish tubules located lateral to the ovaries. After
ovulation and until parturition (December-mid-June), the
uteri of mature females contain yolk-filled eggs which are
readily visible through the now transparent walls of the
greatly stretched uteri. The vaginae remain whitish in
color and are opaque.

Histology

The wall of the oviduct throughout its length con-
sists of an inner mucosa whose luminal border is covered
by a single layer of ciliated columnar epithelium with
interspersed mucoid secreting goblet cells (Fig. 17), an
underlying lamina propria, and an outermost serosa.

The topography of the mucosa is variable in different areas of the oviduct. It is flat throughout the infundibulum and flat with an occasional fold throughout most of the uterus. These folds become increasingly common and deeper, appearing as convulted crypts in the posterior areas of the vagina. Masses of sperm are frequently seen in the inner reaches of these crypts (Fig. 18) where they may remain as long as eight months after insemination, from September to April. The blind tubules that open into the crypts are lined by a single layer of non-ciliated columnar epithelium and frequently accumulate sperm, thereby serving as "seminal receptacles."

The underlying lamina propria contains both inner circular and outer longitudinal layers of smooth muscle, capillaries and small blood vessels (Fig. 19). Seasonally varying numbers of simple, non-branched, tubulo-alveolar glands which appear to fit the serous classification, are present in the lamina propria (Figs. 20-21). They occur in clusters of three to four or as isolated individuals. Some of them open to the luminal surface by short non-ciliated ducts. They have been called uterine glands by previous workers (Giersberg 1922, Boyd 1942) even though their distribution is not restricted to the uterus. A connective tissue serosa forms the outer boundary of the oviduct.

The distal infundibulum is the thinnest section of
the oviduct. Muscle bands that characterize the uterine
and vaginal areas of the oviduct are absent except for a
few circular fibers; uterine glands likewise appear to be
absent.

The topographic arrangements of the uterine and
vaginal muscles vary as a result of the stretching of the
oviduct due to the presence of ova during seven months of
the year. This is particularly evident in the outer longi-
tudinal band which occurs in undulating folds in the pre-
ovulatory uteri and whose thickness in general varies be-
tween 25-50 micra. After the uteri contain eggs, the outer
longitudinal muscles are stretched so that they occur in a
roughly continuous band (11 micra). The thinner inner
circular band is subject to less seasonal folding and varies
between 15-35 micra in thickness.

The oviduct is supplied by several medium sized
arteries from the dorsal aorta which give rise to numerous
smaller vessels in the muscular layers of the lamina
propria. There is a gradual increase in the size and num-
ber of the uterine blood vessels in late March, concomitant
with the onset of rapid embryonic development (Fig. 22,
Table 12) culminating with the appearance of young in mid-
June.

Placenta formation in Sceloporus jarrovi begins
in the latter part of March and is completed by early April.
Allantoplacenta formation results from the superficial
attachment of the allantochorion to the uterine wall (Fig.
23) while the omphaloplacenta (Fig. 24) is formed by a close
apposition of the uterine wall with the chorionic ectoderm.
That their development is progressing is evident because it
is difficult to separate these tissues from the uterine
wall in freshly killed females. That no permanent fusion
occurs is apparent as the uterine and embryonic tissues
cleanly separate after formalin fixation. Detachment also
occurs during gestation so that the young are surrounded
by the allantochorion membrane at birth.

Equal numbers of males and females are produced at
birth (Table 13), the young weigh approximately 0.77 gms
and average 28.0 mm snout-vent length (Tables 14-15).
Gravid females lose approximately 30-40% of their body
weight (Table 16) during parturition.

Seasonal Cycle

September-October.--Changes in the oviduct become
evident as the time of ovulation approaches. A renewal
of ciliated columnar epithelium has occurred and there are
increases in the number of uterine glands (Fig. 20) which
reach their greatest numbers in both the uterus and the
vagina. The epithelium of the hypertrophied glands is

composed of large non-ciliated cells, the apexes of which are contracted toward the lumen of the gland. Nuclei are located within the basal one third of the cells and the cytoplasm is conspicuously filled with secretory granules. Lumina are clear or may be occluded by the distal tips of the swollen glandular cells. The uterine glands show progressive reductions in the amount of intracellular cytoplasm during the course of the gestation period.

January.--The thickness of the muscular layers has decreased due to the stretching caused by the enclosed ova. The ciliated epithelium remains unchanged and the number of uterine glands decreases slightly from the densities observed in October. Large amounts of sperm are found in the crypts created by the foldings of the vaginal mucosa (Fig. 18), and sperm may be seen to penetrate individual epithelial cells. Yolk granules are scattered throughout the oviduct.

April.--The oviduct shows a serious depletion of uterine glands when compared to the October-January organ. Moderate amounts of sperm remain isolated in the seminal receptacles and inner vaginal crypts.

July.--The oviduct is "inactive" at this time. Columnar epithelium is conspicuously collapsed or absent and may have been damaged during parturition. Uterine glands are sparse, the cytoplasm of their epithelial cells

is noticeably depleted (Fig. 21) and the cells are com-
pressed or cuboidally shaped. The lumina are clear and
conspicuously enlarged as compared to October. Areas of
the longitudinal muscle band are thrown into undulations
(Fig. 19) and all traces of sperm are gone from the vagina.

Discussion

It was noted by Cuellar (1966a) that seminal re-
ceptacles of the iguanids occur principally in the middle
and anterior parts of the vagina and are most numerous at
the utero-vaginal transition. In Sceloporus jarrovi stored
sperm was observed only in the deeper folds of vaginal
epithelium.

Sperm storage bestows a distinct advantage among
reptiles, animals in which meetings of the opposite sexes
during the breeding season are often highly irregular.
Storage of viable sperm has been reported for the eastern
box turtle Terrapene carolina (four years, Ewing 1943),
prairie rattlesnake Crotalus viridis (over winter, Rahn
1942), indigo snake Drymarchon corais couperi (four and
one half years, Carson 1945).

As Sceloporus jarrovi has only one brood of young
each year, the seminal receptacles do not function as a
means of assuring fertilization for subsequent clutches
without additional inseminations as in Uta stansburiana

Table 12. Mean monthly weight (gms) of post-ovulatory ova and newborn young
(at birth) from Sceloporus jarrovi, November 1968-June 1969.

Month	Females Examined	Ova (N)	Weight Ova Left Oviduct	Range	95% Confidence Interval
Nov.	1	5	0.275	0.271-0.278	
Dec.	9	26	0.326±0.014	0.273-0.376	0.294-0.358
Jan.	10	34	0.316±0.013	0.266-0.407	0.287-0.345
Feb.	13	41	0.321±0.009	0.267-0.387	0.301-0.341
March	11	41	0.324±0.012	0.279-0.435	0.298-0.350
April	10	36	0.377±0.013	0.326-0.450	0.348-0.408
April 15	8	23	0.508±0.020	0.395-0.632	0.457-0.554
April 24	8	27	0.557±0.021	0.504-0.697	0.506-0.608
May 8	11	33	0.677±0.024	0.526-0.777	0.622-0.731
May 20	8	19	0.750±0.025	0.598-0.828	0.692-0.810
June 8	11	26	0.883±0.025	0.736-1.020	0.829-0.938
Young	16	119	0.822±0.012 (brood)	0.746-0.927	0.797-0.847

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Table 13. Sex ratio for newborn Sceloporus jarrovi.
           (Raw data in Appendix B.)

Year	Litters (N)	Young (N)	Females (N)	Females (%)	Males (N)	Males (%)
1968	10	51	25	49.0	26	51.0
1969	16	119	65	55.0	54	45.0
Total	26	170	90	--	80	--
Mean	13.0	85.0	45	<u>52</u>	40	<u>48</u>

Table 14. Mean weight (gms) for newborn Sceloporus jarrovi.
           (Raw data in Appendix B.)

Year	Number Litters	Number Young	Weight	Range	95% Confidence Interval
1967	15	87	0.77±0.012	0.68-0.86	0.75-0.80
1968	10	51	0.78±0.016	0.69-0.87	0.75-0.82
1969	16	119	0.82±0.012	0.74-0.93	0.79-0.84

Table 15. Mean snout-vent lengths (mm) for newborn
Sceloporus jarrovi. (Raw data in Appendix
B.)

Year	Number Litters	Number Young	Snout-Vent Length	Range	95% Confidence Interval
1967	15	87	27.8±0.222	26.2-29.2	27.3-28.2
1968	10	51	28.0±0.203	27.4-28.8	27.6-28.5
1969	16	119	28.2±0.164	27.5-29.1	27.9-28.6

Table 16. Average % weight loss immediately after birth
for female Sceloporus jarrovi. (Raw data in
Appendix C.)

Year	N	Average % Weight Loss at Parturition	Range	95% Confidence Interval
1967	15	39.3±1.051	34.1-48.9	37.1-41.6
1968	10	32.2±2.622	17.2-41.7	26.3-38.1
1969	16	32.0±1.272	22.8-41.6	29.3-34.7
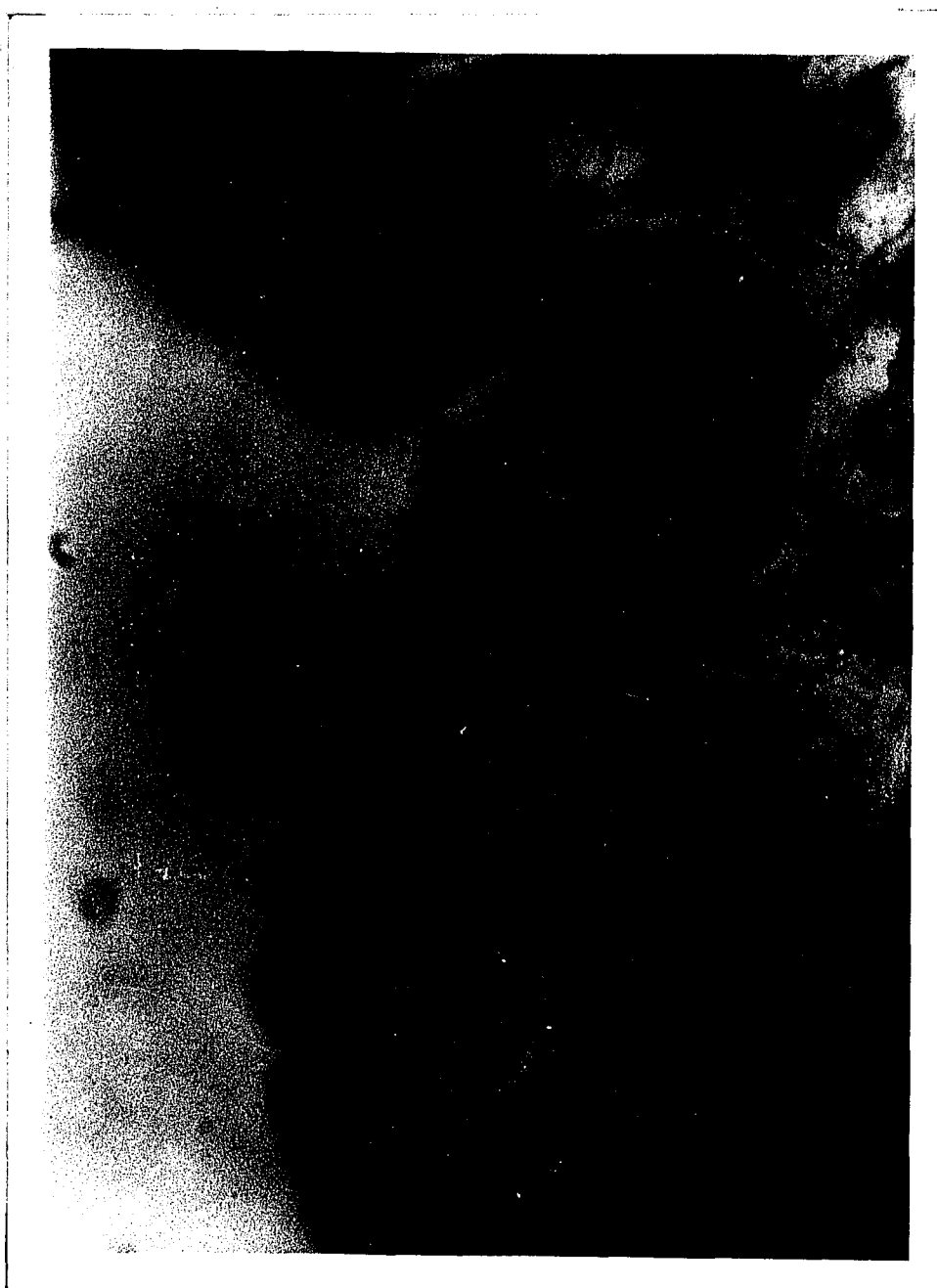
Fig. 17. Oviduct of <u>Sceloporus jarrovi</u>, October 8, 1967.
(Note cillated columnar epithelium with inter-
spersed (arrow) goblet cell, 1920X.)
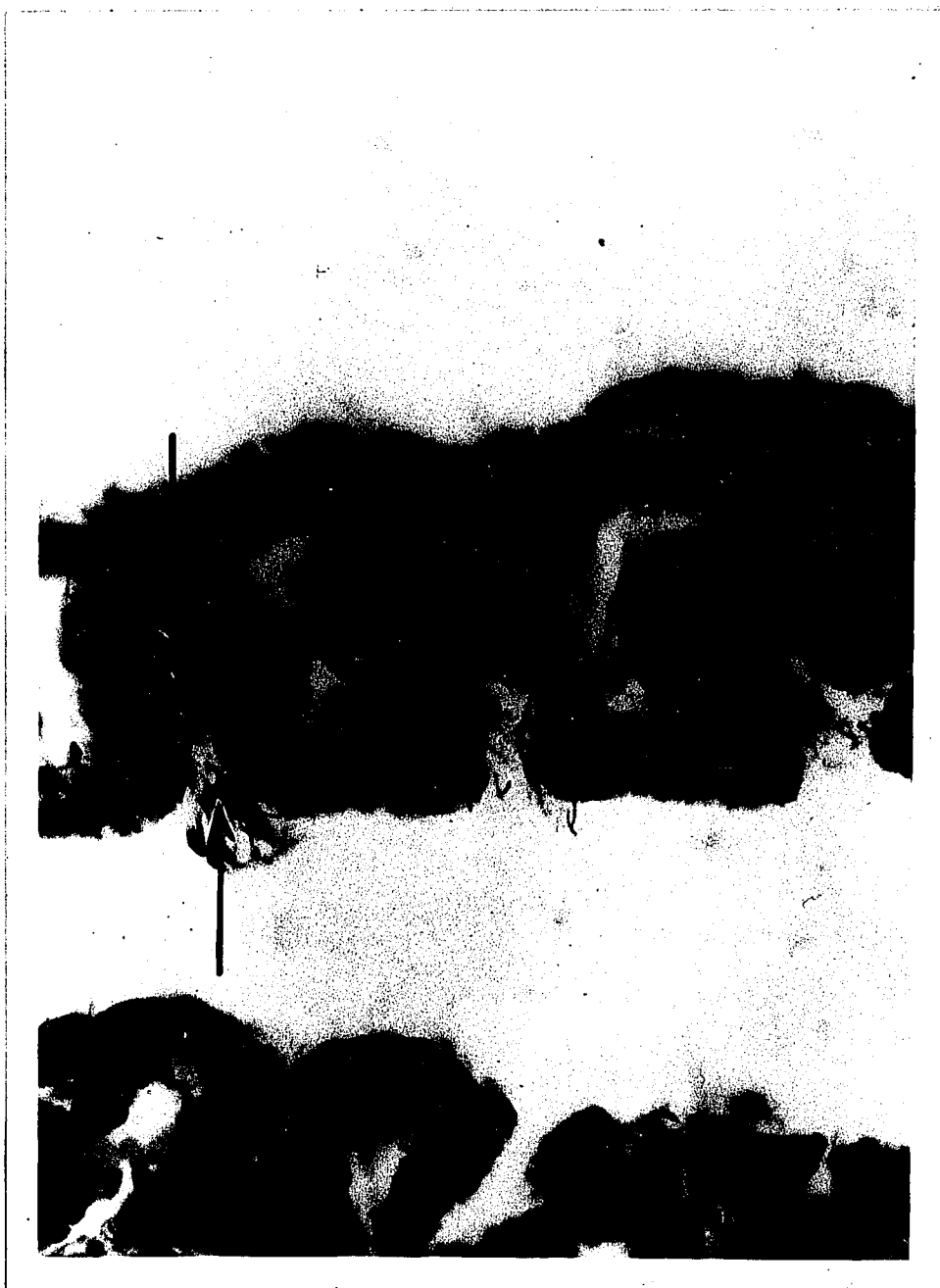
Fig. 18. Sperm storage in *Sceloporus jarrovi* female, January 6, 1968. (Clusters of sperm (arrows) in a mucosal crypt in the vagina, 300X.)
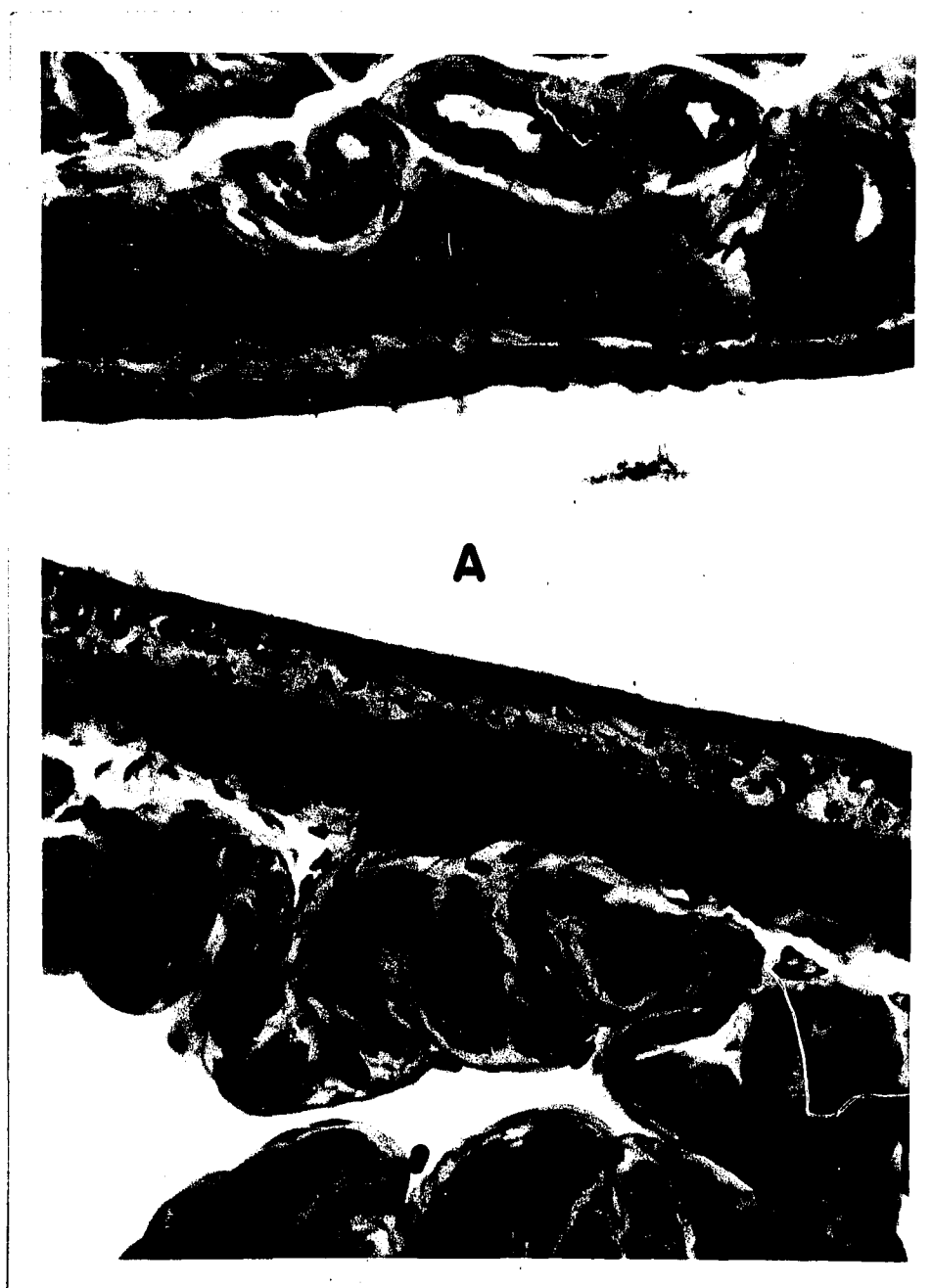
Fig. 19. Uterus of Sceloporus jarrovi, July 1967, cross
          section. (Note lumen (A), circular (B) and
          longitudinal (C) muscle layers, 300X.)
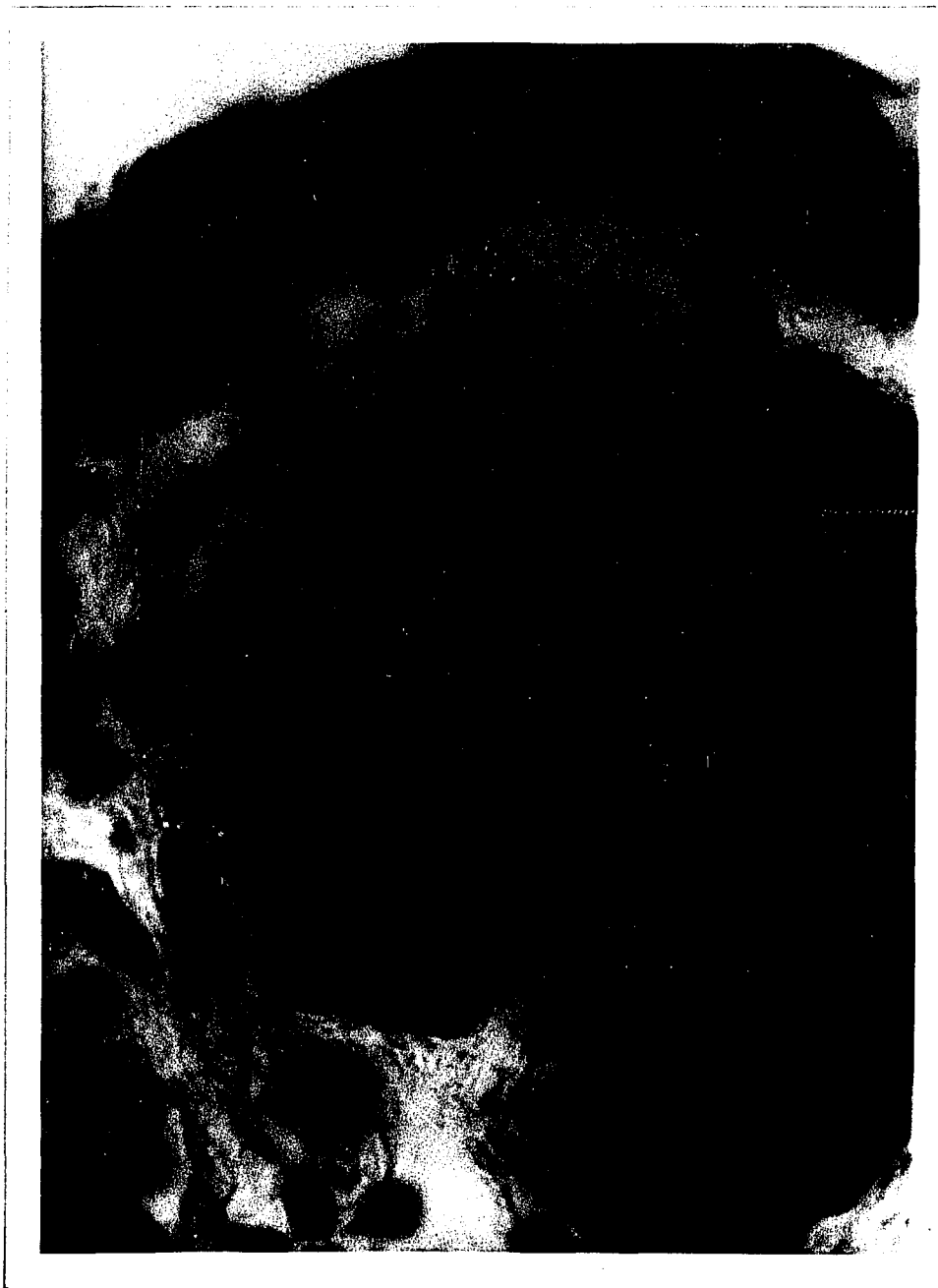
Fig. 20. Uterine gland from Sceloporus jarrovi, October 8,
1967. (Note abundant secretory granules in hyper-
trophied epithelial cells, 1920X.)
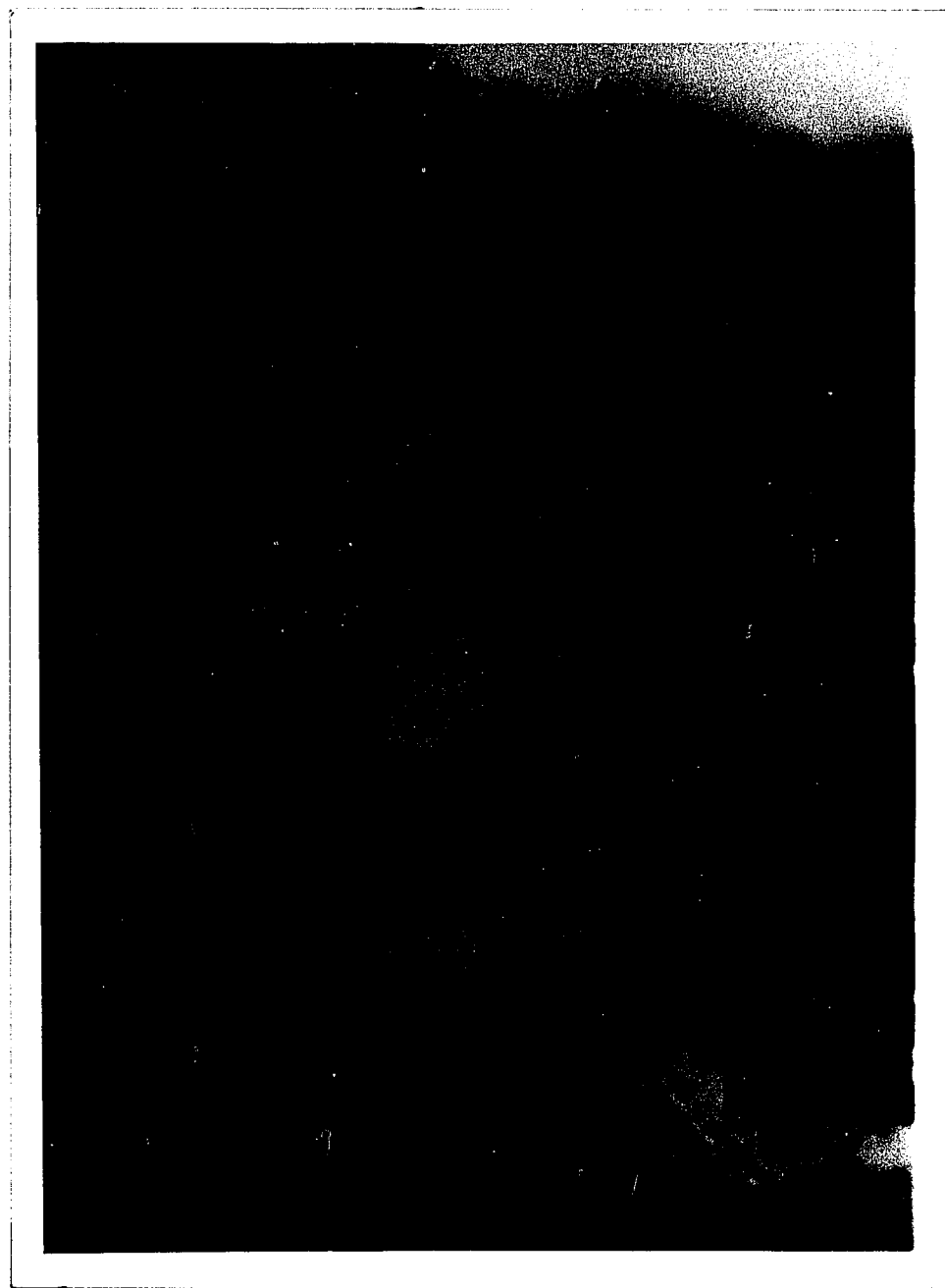
Fig. 21.   Uterine gland from Sceloporus jarrovi, July 8, 1967.   (Note depletion of epithelial cell cytoplasm, 1920X.)
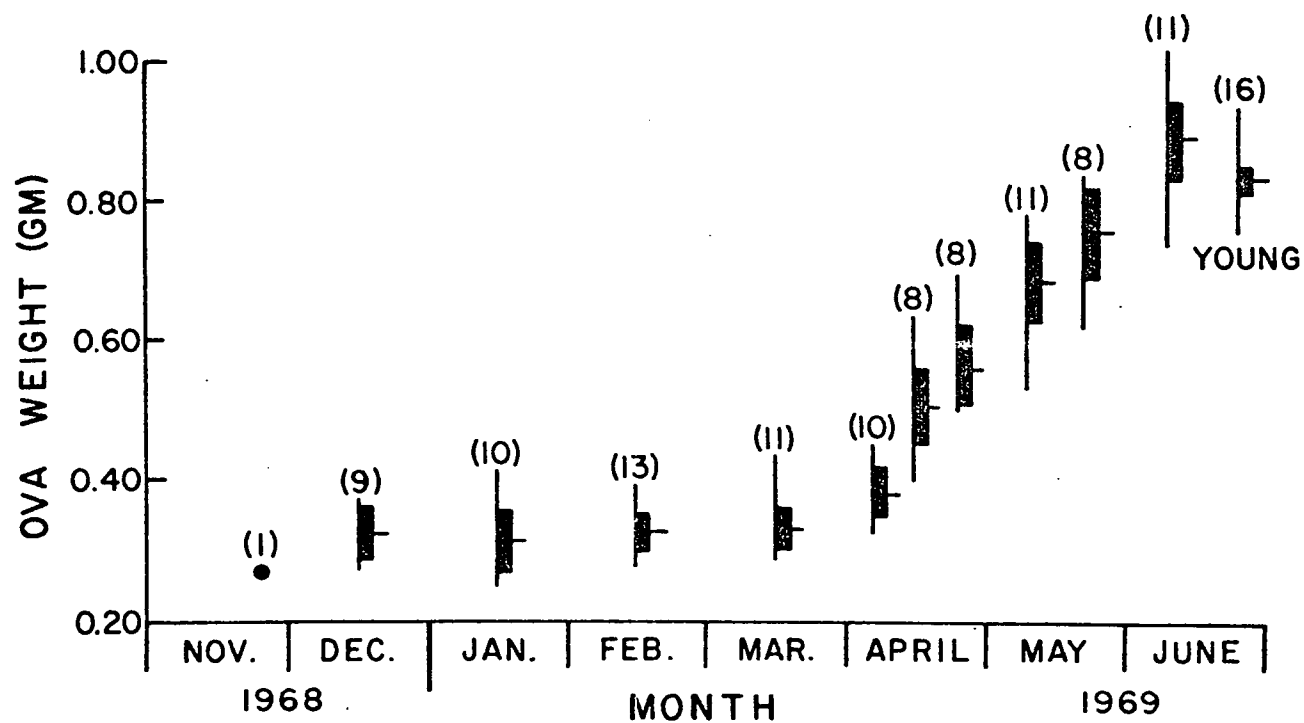
Fig. 22. Mean monthly weight (gms) of post-ovulatory ova from _Sceloporus_ _jarrovi_, November 1968–June 1969.

Fig. 23. Portion of allantoplacenta from Sceloporus jarrovi, April 15, 1969. (The separation of uterine epithelium (A) and allantochorion (B) is the result of fixation, 1920X.)

Fig. 24. Portion of omphaloplacenta from Sceloporus jarrovi,
          April 15, 1969. (Note prominent shell membrane
          (arrow) between chorionic ectoderm (A) and uterus
          (B), 1920X.)

(Cuellar 1966b) and possibly in other lizards that have more than one clutch of eggs per season, e.g., Cnemidophorus sexlineatus (Hoddenbach 1966) and Uma notata (Mayhew 1966a). Moreover, since all traces of sperm are gone from the oviducts of S. jarrovi examined in July there is no chance of a group of eggs being fertilized by sperm from the previous year.

The seminal receptacles of Sceloporus jarrovi actually play an important if not vital role in effecting fertilization. Because ovulation does not occur until late November or early December, by which time the testes are regressing or totally regressed, ova are fertilized by sperm which have been stored in the seminal receptacles for from 1-4 months.

Since the sperm storage areas of Sceloporus jarrovi are located exclusively in the vagina, as is the case for egg-laying Anolis carolinensis (Fox 1963), this organ must be stimulated to expel the stored sperm into the uterus for fertilization to occur. Timing of sperm release may be more critical in shell-secreting oviparous lizards than live-bearing ones. Seminal receptacles of snakes are more advantageously located at the base of the infundibulum (Fox 1956).

Efforts to elucidate the roles played by cilia and other structures of the reptilian oviducts have been

inconclusive. The entrance of the egg into the oviduct
after ovulation is presumably brought about through the
action of cilia as in mammals (Alden 1942, Blandau and
Canado 1958). It was found by Parker (1928) that the
majority of cilia on the oviduct wall of the painted
turtle Chrysemys picta beat toward the cloaca. In contrast,
Crowell (1932) noted groups of cilia in the oviducts of
Phrynosoma cornutum and Sceloporus undulatus that beat
toward the infundibulum, presumably serving to carry sperm
up the oviduct.

Extra-uterine migration of ova is relatively common
in Sceloporus jarrovi (Table 10) and appears to be common
in lizards and perhaps among reptiles in general. Tinkle
(1961) reported that it may occur 20% of the time in Uta
stansburiana while Mayhew (1966b) recorded it in 9% of the
Uma scoparia females he investigated. Its occurrence has
been confirmed in the following reptiles: lizards,
Sceloporus orcutti (Mayhew 1963), Uma inornata (Mayhew
1965), Cnemidophorus hyperythrus beldingi (Bostic 1966),
Cnemidophorus sexlineatus (Hoddenbach 1966) and Uma notata
(Mayhew 1966a); turtles, Terrapene ornata (57%) and T.
carolina (13%) (Legler 1958), and Sternothaerus odoratus
(57%) (Tinkle 1959).

Weekes (1935) described three types of allanto-
placentae for reptiles and their occurrence in certain

Australian lizards. In the first type the partial degenera-
tion of uterine and embryonic epitheial tissue leads to a
close apposition of maternal and embryonic blood streams.
This type occurs in the Australian skinks Lygosoma (Hinulia)
quoyi, L. (Hemiergis) quadrigitatum, Egernia cunninghami,
E. striolata, E. whitei, Tiliqua nigrolutea, T. scincoides,
Mabuja multifasciata, and the New Zealand gecko Hoplodac-
tylus maculatus as described by Boyd (1942).

In the second type the maternal capillaries bulge
at the surface of the uterus as small ridges covered by a
thin layer of glandular epithelium. The uterine epithelium
is reduced and the ectoderm cells of the underlying chorion
are enlarged. This placenta is found among Lygosoma
(Liolepisma) pretiosum, L. (L.) ocellatum and L. (L.)
metallicum.

The third and most highly specialized type occurring,
in Lygosoma (Liolepisma) weeksae L., (L.) entrecasteauxi
and Chalcides tridactylus, is characterized by an elliptical
area in which uterine folds with enlarged epithelial cells
indent the greatly enlarged cells of the chorionic ectoderm.
This placenta can be seen with the naked eye whereas the
other two are visible only in sectioned material.

The allantoplacenta of Sceloporus jarrovi appears
to be a distinctive structure somewhat, but not radically
different from previously described lizard placentae. It

differs from the first two types described by Weekes (1935) in that the uterine epithelium is not reduced. It differs fundamentally from the third type because it lacks the folded areas of the uterine wall that are visible to the naked eye, and the uterine epithelium and chorionic ectoderm cells are not enlarged. While maternal and foetal blood streams are in close proximity, there does not appear to be any invasion of maternal tissue. As has been reported for other lizards by Weekes (1935), Boyd (1942), and Heimlich and Heimlich (1950), the omphaloplacenta of Sceloporus jarrovi diminishes during the gestation period presumably due to the absorption of yolk.

The precise role played by the reptilian placenta has yet to be determined. Weekes (1930, 1935) postulated that the allantoplacenta may be used by the embryo for respiration and that the omphaloplacenta may function to absorb water, thereby facilitating the uptake and utilization of yolk by the embryos. It appears plausible that similar roles may be carried out by the placentae of Sceloporus jarrovi. Bauchot (1965) provides a thorough review, written in French without English summary, of the contributions of various workers to our knowledge of the structure and function of the reptilian placenta.

In reptiles expulsion of the embryos during parturition is most likely achieved through contractions of

the oviduct musculature as has been verified in mammals
by Alden (1942). This appears to be true for Sceloporus
jarrovi, as Carpenter (1960) observed "labor movements"
in the form of violent contractions in the abdominal region
of female S. jarrovi just before parturition.

Oviducts of Sceloporus jarrovi resume their normal
cylindrical shapes almost immediately after parturition.
This contrasts with the situation in the Australian skink
Lygosoma (Hinulia) quoyi in which Weekes (1927a) reported
that the oviducts fail to regain their natural shape.

THE FAT BODIES

Gross Morphology

The fat bodies are paired yellowish structures located at the rear of the body cavity where they are attached to the ventral body wall. Their size varies with the nutritional state of the animal and the season in which they are examined (Figs. 25-30, Tables 17-20).

Histology

The undepleted fat cells are spherical to rectangular with the cytoplasm typically displaced to the periphery by a single large fat droplet. The nucleus is surrounded by a small amount of cytoplasm and is usually pressed against the cell wall. Connective tissue penetrates between the fat cells and serves as a bed for large numbers of capillaries and blood vessels that are normally present in the fat body.

During the spring, fat bodies of the majority of lizards examined are greatly reduced with numbers and sizes of individual cells seriously depleted in both sexes (Fig. 29, Tables 17-20).

Seasonal Cycle

September-October.--Fat bodies and fat cells reach maximum weight during early fall (Figs. 25-27, Tables 17-20), depending on year and related to the onset of yolk deposition. At this time the cell walls are stretched by the enclosed lipid and frequently crumble during sectioning. It is noteworthy that fat body weights are higher in females than males during this period (Tables 17-18) and that maximum fat body sizes for males occur earlier (August) than in females (September).

January.--Fat body weights are reduced and some of the fat cells already show their first signs of depletion (Figs. 25-26, 28, Tables 17-20).

April.--Fat bodies are reduced to their smallest size during the spring (Figs. 25-26, 29, Tables 17-20). Involution may be total, or so extreme as to render the organ barely recognizable as fat body, with diameters of cells shrinking to as little as 20 micra compared to 50 micra in October. Intercellular areas have greatly increased and are occupied by connective tissue and capillaries.

The slower recovery of the fat bodies in females as compared to males (Fig. 25, Tables 17-18) is probably due in part to the increased demands placed on the females by the unborn young. After parturition occurs in June,

recovery proceeds rapidly in females with total recrudes-
cence completed by early July.

July.--Lizards have received sufficient nutrition
so that fat body recrudescence is completed (Figs. 25-26,
30, Tables 17-20). Thicknesses of the fat cell walls are
slightly reduced as compared to April and the intercellular
aggregations of connective tissue that characterized the
depleted April organ have disappeared, restoring its
characteristic "chicken wire" or "signet cell" appearance
to the fat body section.

Discussion

It has long been known (Gadow 1901) that the fat
bodies of certain temperate zone lizards follow a seasonal
cycle with maximum sizes reached at the onset of reproduc-
tion, followed by a rapid depletion. Experimental evidence
indicating that the lipid reserves within these bodies are
passed on to the organs of reproduction and that adequate
fat reserves are important for the successful completion
of the normal reproductive cycle has been recently supplied
by Hahn and Tinkle (1965) working with Uta stansburiana,
and by Smith (1968) who worked with the teiid lizards
Ameiva festiva and Ameiva quadrilineata.

By performing experiments on Uta stansburiana in-
volving removal of fat bodies in some females and sham

Table 17. Fat body and body weights (gms) for ratios % fat body weight/body weight for female _Sceloporus_ _jarrovi_, April 1968-October 1969. (Data graphed in Fig. 25.)

Month	N	Total Fat Body		Body Weight		Ratio Fat body wgt./body wgt.		95% Confidence Interval
		Mean	Range	Mean	Range	Mean	Range	
April	11	0.061	(0.012-0.198)	15.06	(7.96-24.38)	0.362 ± 0.087	(0.109-0.991)	0.169-0.555
May	9	0.081	(0.024-0.190)	16.33	(9.23-28.53)	0.457 ± 0.046	(0.250-0.663)	0.351-0.563
June	12	0.071	(0.000-0.366)	14.68	(8.54-27.01)	0.601 ± 0.143	(0.000-1.585)	0.287-0.915
July	17	0.446	(0.213-0.876)	14.13	(10.16-20.31)	3.118 ± 0.270	(1.750-5.380)	2.549-3.698
Aug.	10	0.572	(0.269-1.014)	15.43	(11.38-20.66)	3.591 ± 0.390	(1.964-5.050)	2.709-4.473
Sept.	11	0.883	(0.423-1.499)	18.63	(12.31-23.62)	4.667 ± 0.270	(3.432-6.351)	4.066-5.268
Oct.	16	0.586	(0.345-0.912)	17.03	(8.39-25.89)	3.276 ± 0.221	(0.291-4.056)	2.806-3.746
Nov.	12	0.317	(0.174-0.542)	15.78	(7.30-25.71)	2.051 ± 0.113	(1.343-2.632)	1.803-2.299
Dec.	10	0.146	(0.090-0.320)	10.01	(5.67-15.08)	1.478 ± 0.178	(0.922-2.598)	1.078-1.878
Jan.	10	0.215	(0.033-0.357)	18.80	(9.19-21.46)	1.294 ± 0.182	(0.356-2.204)	0.983-1.605
Feb.	13	0.172	(0.016-0.331)	14.03	(8.41-18.28)	1.165 ± 0.156	(0.452-1.922)	0.826-1.504
March	11	0.191	(0.036-0.571)	16.98	(13.21-21.07)	1.069 ± 0.247	(0.250-2.575)	0.822-1.306
April	15	0.057	(0.005-0.200)	16.64	(6.49-25.73)	0.322 ± 0.074	(0.060-0.617)	0.163-0.481
May	15	0.071	(0.000-0.366)	17.07	(7.28-27.96)	0.160 ± 0.027	(0.044-0.407)	0.103-0.217
June	13	0.037	(0.003-0.130)	15.39	(7.86-23.29)	0.230 ± 0.073	(0.032-0.890)	0.071-0.389
July	12	0.136	(0.050-0.270)	12.61	(7.86-20.16)	1.057 ± 0.078	(0.670-1.450)	0.888-1.226
Aug.	15	0.394	(0.010-1.440)	14.18	(7.35-24.71)	2.562 ± 0.351	(0.144-5.828)	1.787-3.338
Sept.	13	0.486	(0.281-0.946)	14.87	(9.76-29.20)	3.292 ± 0.194	(2.132-4.400)	2.868-3.716
Oct.	11	0.834	(0.510-1.324)	16.96	(14.08-21.22)	4.908 ± 0.350	(3.188-6.667)	4.127-5.689

Table 18. Fat body and body weights (gms) for ratios % fat body weight/body weight for male *Sceloporus jarrovi*, April 1968-October 1969. (Data graphed in Fig. 25.)

Month	N	Total Fat Body		Body Weight		Ratio Fat body wgt./body wgt.		95% Confidence Interval
		Mean	Range	Mean	Range	Mean	Range	
April	5	0.057	(0.018-0.110)	18.60	(7.68-27.57)	0.326	(0.118-0.601)	
May	9	0.084	(0.003-0.210)	16.86	(8.83-31.42)	0.421±0.098	(0.031-0.975)	0.196-0.646
June	12	0.162	(0.000-0.688)	16.57	(11.42-26.12)	0.805±0.228	(0.000-2.805)	0.304-1.306
July	16	0.556	(0.222-1.100)	21.16	(14.00-29.72)	2.518±0.231	(0.987-3.961)	2.026-3.010
Aug.	10	0.664	(0.118-1.513)	20.51	(15.39-28.20)	3.067±0.534	(0.700-5.365)	1.860-4.274
Sept.	11	0.631	(0.133-1.368)	25.91	(17.63-34.08)	2.375±0.302	(0.754-4.014)	1.703-3.047
Oct.	18	0.535	(0.041-1.453)	21.80	(9.08-35.18)	2.131±0.258	(0.045-4.130)	1.587-2.675
Nov.	12	0.286	(0.126-0.460)	20.31	(10.69-26.18)	1.405±0.117	(0.636-1.908)	1.148-1.662
Dec.	14	0.124	(0.040-0.188)	13.04	(6.00-22.10)	1.137±0.189	(0.285-2.677)	0.829-1.445
Jan.	10	0.138	(0.065-0.278)	14.89	(8.31-23.42)	1.028±0.135	(0.387-1.699)	0.723-1.333
Feb.	15	0.159	(0.030-0.340)	19.11	(6.42-28.93)	0.798±0.115	(0.310-1.842)	0.552-1.044
March	11	0.063	(0.014-0.150)	14.75	(7.49-21.68)	0.448±0.087	(0.170-0.939)	0.255-0.641
April	15	0.056	(0.012-0.221)	16.04	(8.12-23.42)	0.327±0.072	(0.089-0.970)	0.173-0.481
May	15	0.026	(0.000-0.084)	15.55	(9.19-25.20)	0.169±0.038	(0.000-0.445)	0.088-0.250
June	14	0.098	(0.010-0.202)	15.74	(9.73-23.10)	0.595±0.092	(0.106-1.150)	0.397-0.793
July	12	0.168	(0.055-0.274)	17.49	(9.31-26.50)	0.810±0.093	(0.382-1.497)	0.608-1.012
Aug.	15	0.361	(0.020-1.057)	17.54	(10.62-29.33)	1.962±0.305	(0.165-3.750)	1.307-2.616
Sept.	12	0.362	(0.094-0.768)	19.16	(12.87-26.28)	1.816±0.269	(0.631-3.667)	1.223-2.409
Oct.	11	0.495	(0.052-0.965)	20.08	(9.93-33.32)	2.251±0.291	(0.529-3.762)	1.603-2.900

Table 19. Fat body cell size data (micra) for female
           Sceloporus jarrovi, April 1968-January 1969.
           (Data graphed in Fig. 26.)

Animal	Cells Measured	Mean Micra	Monthly Mean Micra	95% Confidence Interval
January 1969				
1	20	22.8	34.4±2.131	29.4-39.4
2	20	29.8		
3	20	32.4		
4	20	35.1		
5	20	36.1		
6	20	39.3		
7	20	39.4		
8	20	40.9		
April 1968				
1	20	14.4	25.9±2.515	20.0-31.8
2	20	20.9		
3	20	22.4		
4	20	23.2		
5	20	27.1		
6	20	30.9		
7	20	32.9		
8	20	36.0		

Table 19. (Continued)

Animal	Cells Measured	Mean Micra	Monthly Mean Micra	95% Confidence Interval
July 1968				
1	20	34.9	44.6±3.099	37.3-51.9
2	20	36.0		
3	20	36.7		
4	20	43.0		
5	20	43.9		
6	20	51.4		
7	20	52.3		
8	20	58.7		
October 1968				
1	20	43.6	51.0±1.752	46.9-55.1
2	20	45.7		
3	20	47.9		
4	20	50.9		
5	20	52.6		
6	20	54.5		
7	20	55.3		
8	20	57.9		

Table 20. Fat body cell size data (micra) for male
Sceloporus jarrovi, April 1968-January 1969.
(Data graphed in Fig. 26.)

Animal	Cells Measured	Mean Micra	Monthly Mean Micra	95% Confidence Interval
January 1969				
1	20	32.6	34.9±1.092	32.3-37.5
2	20	32.6		
3	20	33.5		
4	20	33.5		
5	20	33.8		
6	20	33.8		
7	20	39.9		
8	20	39.9		
April 1968				
1	20	13.7	18.1±1.196	15.3-20.9
2	20	15.2		
3	20	15.7		
4	20	16.4		
5	20	19.5		
6	20	20.1		
7	20	20.4		
8	20	23.8		

Table 20.   (Continued)

Animal	Cells Measured	Mean Micra	Monthly Mean Micra	95% Confidence Interval
July 1968				
1	20	36.7	44.0±1.709	40.0-48.0
2	20	39.4		
3	20	40.4		
4	20	41.0		
5	20	42.4		
6	20	46.5		
7	20	52.7		
8	20	53.1		
October 1968				
1	20	40.8	47.9±2.230	42.6-53.2
2	20	43.1		
3	20	44.5		
4	20	45.5		
5	20	47.1		
6	20	47.8		
7	20	56.8		
8	20	58.3		
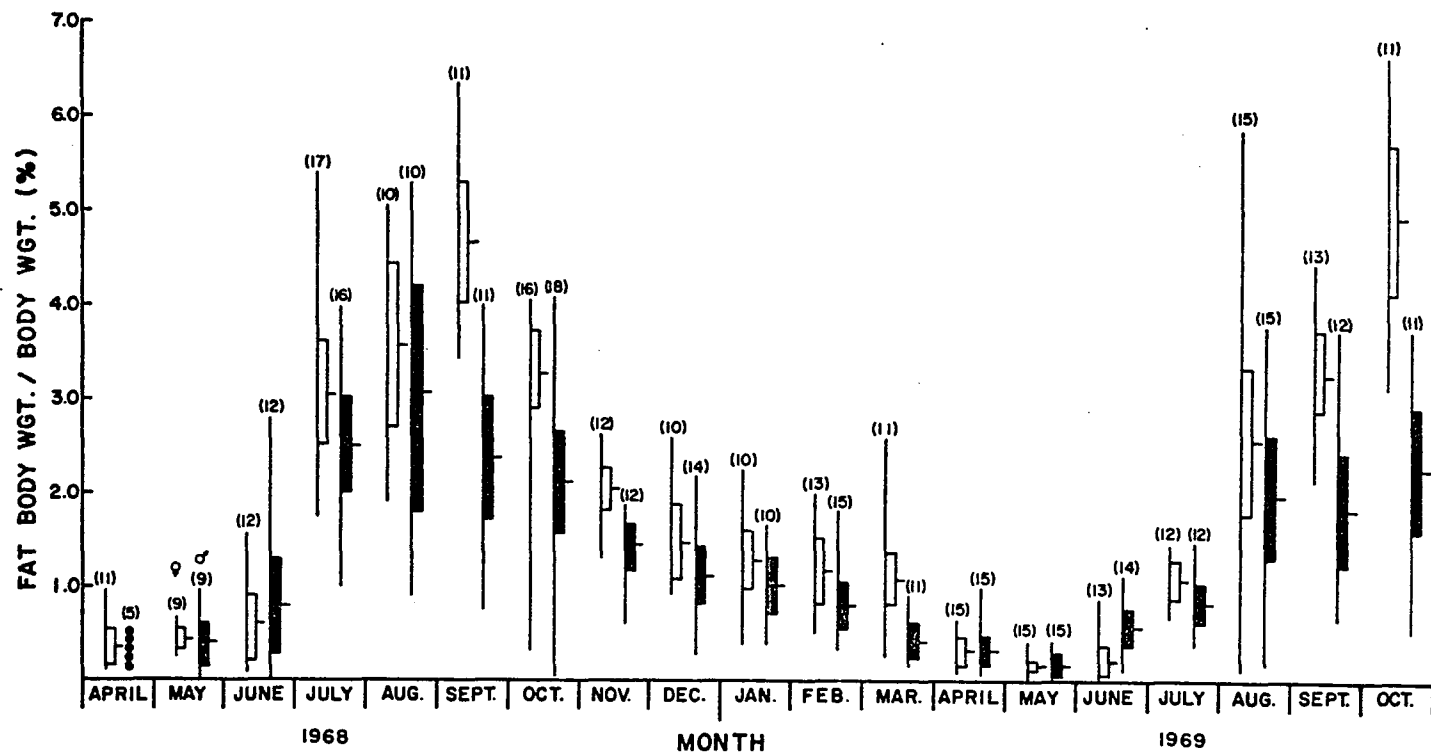
Fig. 25. Modified Dice-Lerras graph showing seasonal changes in % fat body/body weight (gms) for _Sceloporus jarrovi_, April 1968-October 1969. (Data from Tables 17-18. Bars represent 95% confidence intervals, females unshaded, males shaded.)
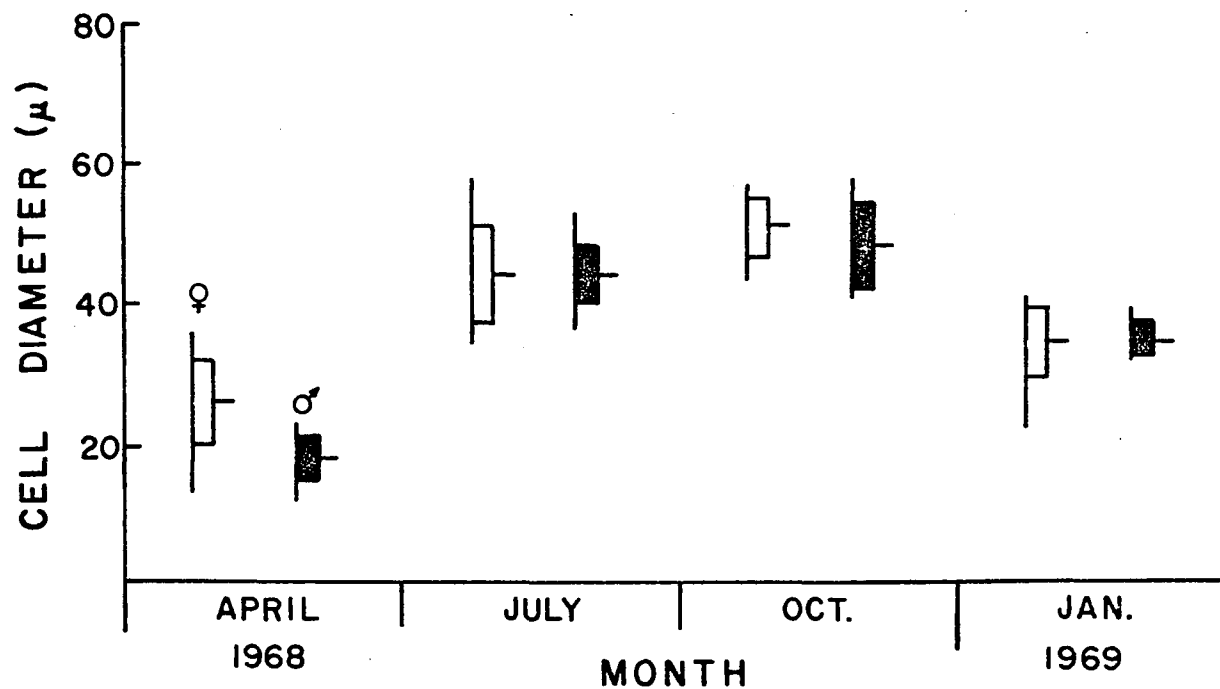
Fig. 26. Modified Dice-Lerras graph showing seasonal variation in fat body cell size for <u>Sceloporus jarrovi</u> females and males, April 1968-January 1969. (Data from Tables 19-20. Bars represent 95% confidence intervals, females unshaded, males shaded.)
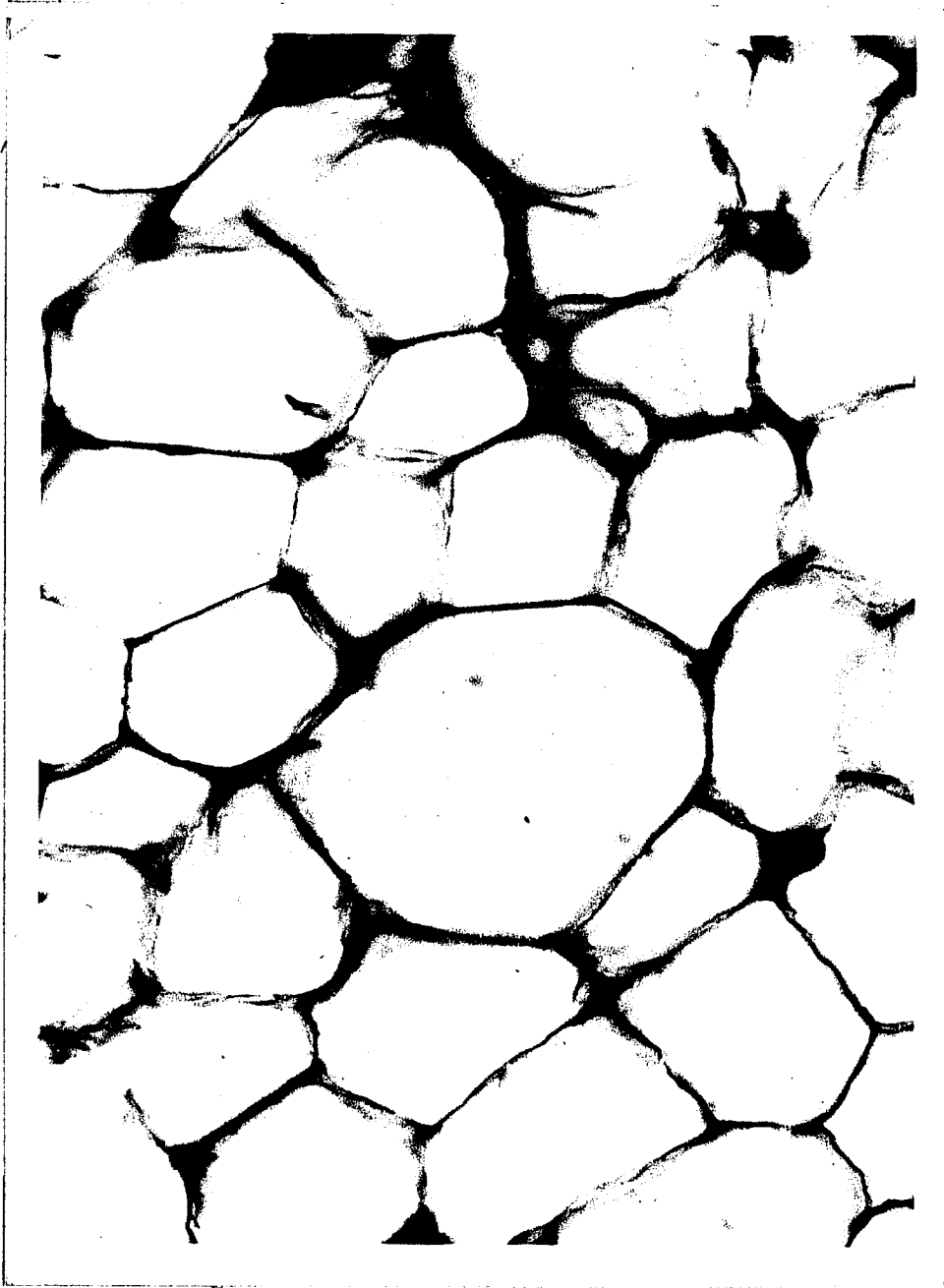
Fig. 27.   Fat body cells, maximum October size, from
           Sceloporus jarrovi female, October 9, 1968.
           (760X)
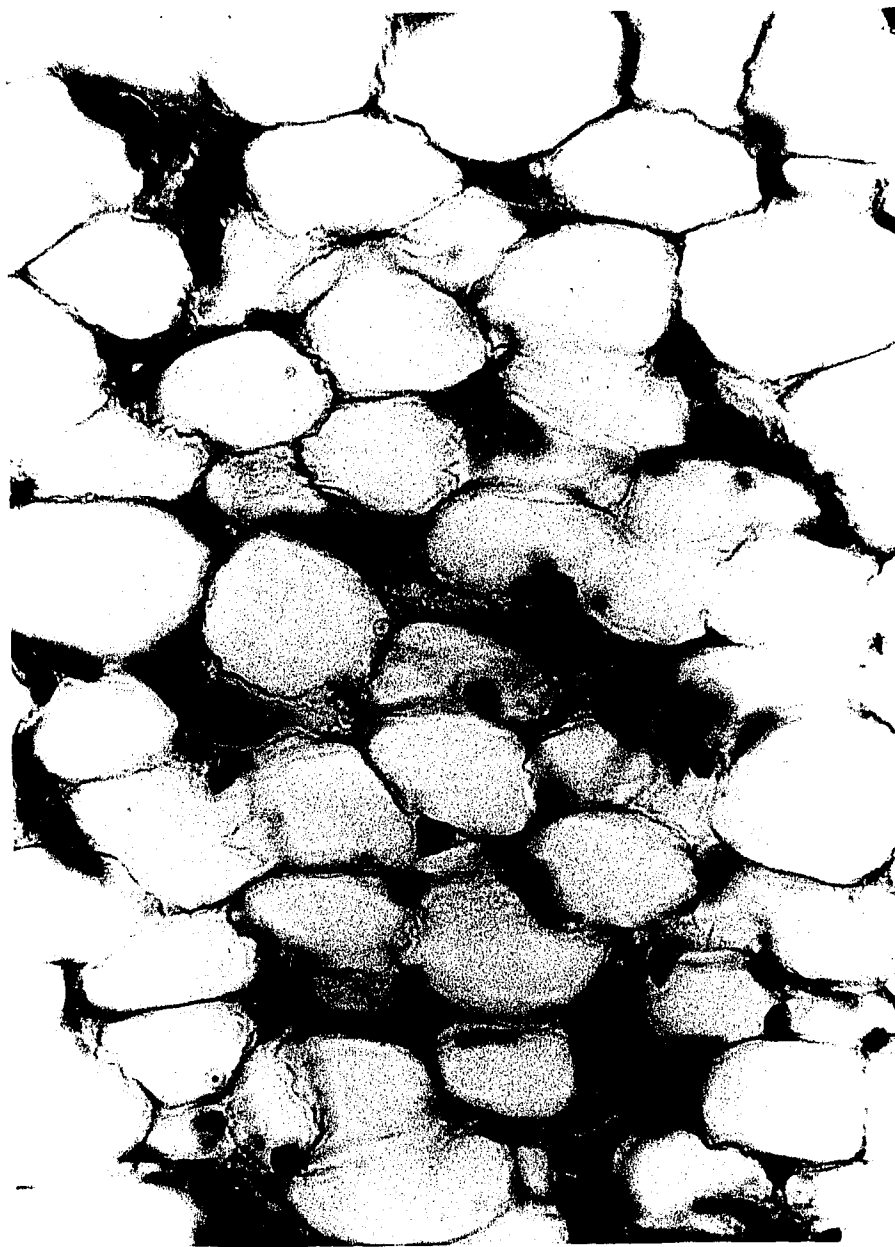
Fig. 28.   Fat body cells, reduced size, from _Sceloporus_
jarrovi male, January 8, 1969. (Compare with
Fig. 27, October, 760X.)

Fig. 29.   Section through depleted fat body from *Sceloporus jarrovi* male, April 30, 1968.   (760X)
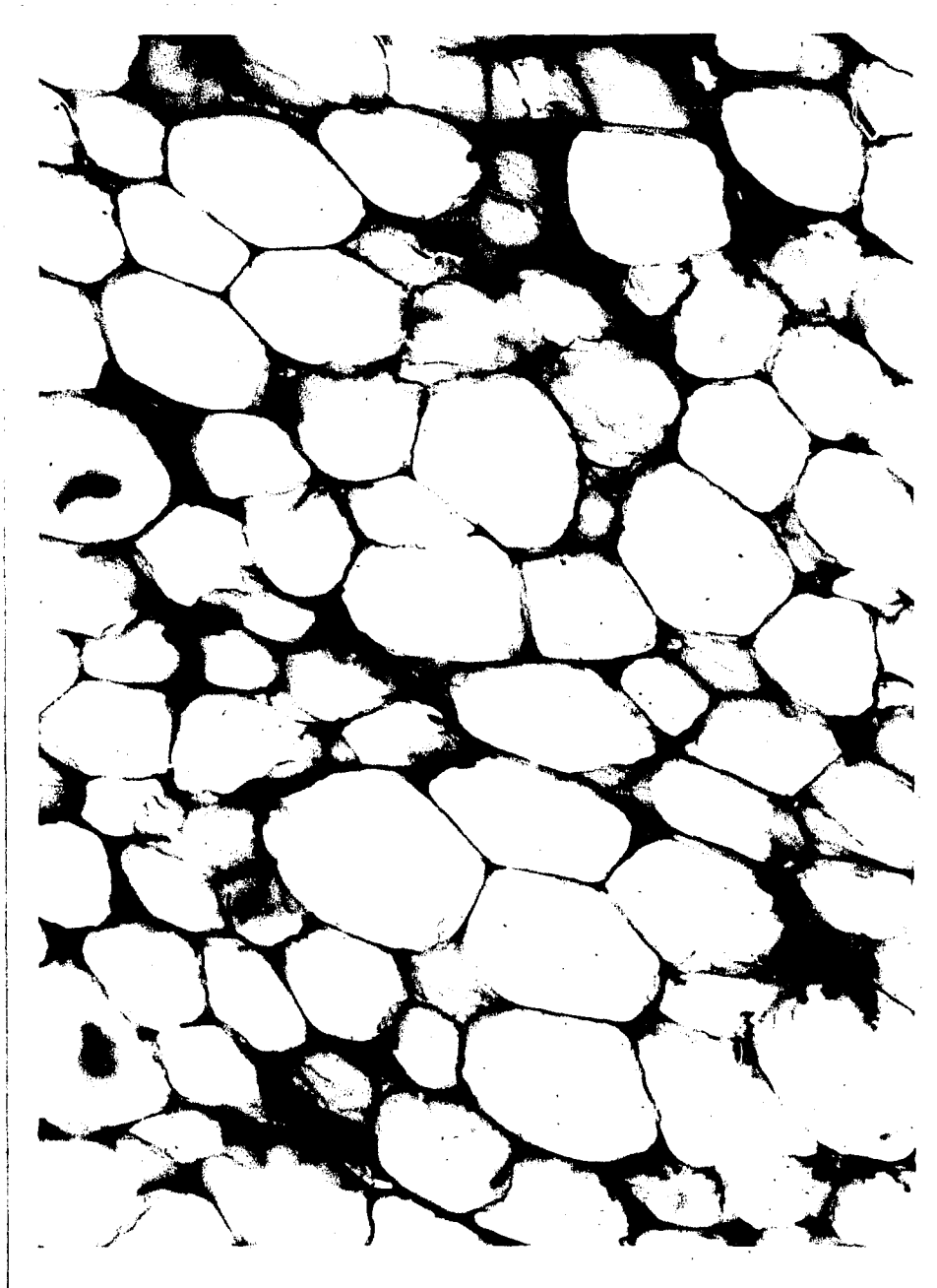
Fig. 30.   Fat body recrudescence, completed in Sceloporus
           jarrovi female, July 8, 1968.   (760X)

operations on others, Hahn and Tinkle (1965) were able to demonstrate that females deprived of fat reserves were either unable to produce yolked follicles, or, if vitellogenesis had begun prior to the operations, yielded a higher proportion of atretic follicles when compared to either field controls or sham operated animals. They also reported that the amount of extractable lipid from the fat body before vitellogenesis is nearly equivalent to the lipid found in a typical egg clutch. Smith (1968) found that removal of fat bodies from females of Ameiva festiva and A. quadrilineata resulted in atresia of all deuteroplasmically active follicles.

While it is clear that sufficient fat reserves are important in ensuring adequate yolk deposition in females, the role played by the fat bodies in the recrudescence of the testis has yet to be determined. It was noted by Miller (1954) that females from a population of Xantusia vigilis with depleted fat bodies did not deposit yolk and failed to breed whereas spermiogenesis occurred in the males despite a relatively poor nutritional status.

It is clear that the general problem of female fertility and winter fat tissue status in lizards is directly related to diet and dietary intake. The situation in this population (Kitt Peak) and in the Chiricahua Mountains was earlier studied by C. H. Lowe (unpublished),

after discovering that <u>Sceloporus jarrovi</u> was remarkable
among North American mountain lizards in being winter ac-
tive. Under winter conditions, few insects are available
in the mountainous areas inhabited by this species and
dietary intake is severely reduced. During mid-day observa-
tions with field glasses, Lowe observed individuals of both
sexes to dart quickly over to and eat the occasional ants
that came into their view during relatively warm winter
days in December and in February. A few parts of ants were
the only insect remains that he found in the stomachs that
were not empty (11%) in a population sample for the three
winter months of December, January, and February. I have
been able to verify Lowe's work with collection of animals
from the same population during December-February; the
stomachs of these contained either little or no insect
material in contrast to the full and distended stomachs
of summer animals. The large amounts of the summer-fall
stored fat are completely utilized by the early spring of
the following year, ordinarily depleting the fat bodies of
both sexes by March. It remains questionable whether
certain individuals showing serious fat body depletion as
early as January (Tables 17-20) would have been able to
survive the remainder of the winter into March. Part of
the winter fat loss in females is due to energy expended
in the maintenance of ova.

Hahn and Tinkle (1965) found that female <u>Uta</u>
<u>stansburiana</u> store as much as 3-4% of their body weight in
the fat bodies during fall and early winter. This propor-
tion remains constant in early winter until the onset of
yolk deposition (February) indicating that fat reserves
are not being utilized to meet metabolic demands. Males
have a similar fat cycle, but fat bodies are much smaller,
with their weight rarely exceeding 1% of body weight.
Larger quantities of stored fat in females is a relatively
common phenomenon among reptiles in general.

It is concluded by Hahn and Tinkle (1965) that the
adaptive significance of the fat body cycle in <u>Uta</u> <u>stans-</u>
<u>buriana</u>, which normally has several clutches of eggs a
season, lies in its usefulness as an aid to early reproduc-
tion. By effective utilization of lipoidal reserves of the
fat bodies, females are able to begin vitellogenesis early
in the year (mid-February) at which time food is scarce.
Offspring from this early egg clutch have sufficient time
for growth so that they are sexually mature by the fol-
lowing year.

Smith (1968) found percentages of total fat body
weight higher in females than males of the teiid lizards
<u>Ameiva</u> <u>festiva</u> and <u>A. quadrilineata</u>. The fat bodies ap-
parently serve as a means of supplying nutrition to support

vitellization during periods when the lizards are, for example, inactive as a result of inclement weather.

Dessauer (1955) reported a seasonal fat cycle for Anolis carolinensis similar to the cycle of Sceloporus jarrovi in that maximum size of fat bodies occur during the fall, with minimum size reached in early spring. The fat bodies of A. carolinensis in contrast to those of Uta stansburiana (Hahn and Tinkle 1965) are probably utilized for winter survival rather than as a source for yolk deposition because ovarian weight remains minimal throughout autumn and winter. As is the case for the previously discussed lizards, females accumulate more fat than males during the period of maximum size of the fat bodies.

It appears from Hoddenbach's (1966) study on Cnemidophorus sexlineatus that the fat bodies are utilized during vitellogenesis as there is a size decrease in these structures on emergence from hibernation concomitant with the beginnings of yolk deposition. No data are presented for sexual differences in fat storage.

The greater amounts of stored fat in female Sceloporus jarrovi are initially utilized during the period of vitellogenesis which is underway by late August. Extensive utilization of fat deposits are made by females during this period even though food is still plentiful, suggesting that the fat bodies serve as a necessary source

of concentrated lipid reserves whose utilization is needed for the completion of vitellogenesis. Apparently sufficient nutriments for this process cannot be directly obtained from foodstuffs as it would be advantageous for females not to partially deplete their fat reserves before the onset of winter.

It should not go unnoticed that Tinkle (1962) found that reproductive females of the rattlesnake Crotalus atrox, which undergo a biennial reproductive cycle in northwestern Texas, contain 50% more stored fat than non-reproductive females.

SUMMARY AND CONCLUSIONS

The ovaries of Sceloporus jarrovi undergo a sea-
sonal cycle in which yolk deposition occurs in September-
October, and is followed by ovulation in late November.
One corpus luteum forms from each ruptured follicle and
remains until parturition after which time rapid degenera-
tion commences. Follicular atresia is common during the
spring and absent during the summer and early fall. Gran-
ulosal cells play an active role in follicular atresia, in
luteal cell formation, and may also be involved in yolk
deposition.

Storage of sperm plays an important role in ef-
fecting fertilization as ovulation occurs after the testes
are regressed. Sperm may remain in vaginal pockets until
as late as April. Embryonic development beyond the blasto-
derm stage is delayed until April at which time formation
of the allantoplacenta and omphaloplacenta are completed.
Young are born in mid-June after a gestation period of
roughly seven months. Equal numbers of males and females
are produced at birth. Females may lose 30% of their
weight during parturition.

Uterine glands undergo a distinct cycle. They
are secretory during the fall and winter and show a

progressive decrease in their numbers and intracytoplasmic secretions in the spring and summer.

Fat bodies of females and males undergo a seasonal cycle in which maximum cellular sizes and fat body weights are reached in early autumn, minimum sizes occur by spring, and recrudescence is completed by July. Females accumulate higher fat reserves in the fat bodies during early autumn than do males; this extra fat is presumably utilized in vitellogenesis.

APPENDIX A

DISTRIBUTION OF OVA AND CORPORA LUTEA FOR

SCELOPORUS JARROVI FEMALES, NOVEMBER 1968-JUNE 1969

An. No.	Snout-Vent	Right		Left	
		Ova	Corpora Lutea	Ova	Corpora Lutea

November 1968

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
1	71	5	5	2	2
2	75	4	3	3	4
3	77	3	3	3	3
4	77	4	4	4	4
5	90	6	6	3	3

December 1968

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
1	61	2	2	1	1
2	63	3	3	3	3
3	69	2	2	2	2
4	73	3	4	3	2
5	75	2	3	3	2
6	76	4	3	3	4
7	77	4	4	4	4
8	83	5	5	5	5

January 1969

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
1	68	2	3	2	1
2	74	3	3	3	3
3	75	4	2	2	4
4	75	4	3	4	5
5	78	4	4	3	3
6	78	4	2	4	6
7	81	4	3	4	5
8	82	4	4	3	3
9	83	4	3	4	5
10	84	6	6	5	5

An. No.	Snout-Vent	Right			Left		
		Ova	Corpora Lutea		Ova	Corpora Lutea	

February 1969

1	59	1	0		1	2	
2	63	2	2		2	2	
3	66	2	2		1	1	
4	70	3	3		2	2	
5	71	4	4		3	3	
6	74	3	3		3	3	
7	77	4	4		3	3	
8	77	4	2		3	5	
9	78	3	4		5	4	
10	78	4	4		4	4	
11	79	4	4		5	5	
12	79	6	5		4	5	
13	80	4	4		4	4	

March 1969

1	72	3	3		3	3	
2	74	4	4		3	3	
3	75	3	3		3	3	
4	76	3	2		3	4	
5	76	4	4		3	3	
6	76	3	2		3	4	
7	80	4	4		4	4	
8	81	4	4		4	4	
9	83	4	4		5	5	
10	84	6	6		4	4	
11	86	4	5		5	4	

April 1969

1	58	1	1		1	1	
2	62	2	1		1	2	
3	64	1	0		2	3	
4	75	3	2		3	4	
5	75	4	2		2	4	

An. No.	Snout-Vent	Right		Left	
		Ova	Corpora Lutea	Ova	Corpora Lutea

April 1969

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
6	78*	3	3	4	5
7	78	3	3	4	4
8	78	4	4	4	4
9	79	4	5	4	3
10	81	4	3	3	4
11	83	5	5	4	4
12	83	4	4	5	5
13	83	8	6	4	6
14	84	6	5	5	6
15	84	5	7	6	4

May 1969

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
1	61*	1	2	1	1
2	61	2	2	1	1
3	61	2	1	1	2
4	65	2	2	2	2
5	71	3	2	2	3
6	72	3	1	2	4
7	74	4	3	2	3
8	76	3	3	3	3
9	77	3	2	3	4
10	78	5	4	2	3
11	79	4	4	3	3
12	81	5	5	3	3
13	83	5	4	4	5
14	83	5	4	4	5
15	84	5	5	5	5
16	85	5	5	5	5

June 1969

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
1	60	1	1	2	2
2	68	2	2	1	1
3	70	2	3	2	1
4	71*	3	4	1	1

*Indicates reabsorption of ova.

An. No.	Snout-Vent	Right		Left	
		Ova	Corpora Lutea	Ova	Corpora Lutea

<div align="center">June 1969</div>

An. No.	Snout-Vent	Ova	Corpora Lutea	Ova	Corpora Lutea
5	73*	2	2	1	3
6	73	2	2	2	2
7	74	5	5	2	2
8	75	3	1	3	5.
9	76	4	4	2	2
10	80*	5	6	3	3
11	82	5	5	4	4
12	83*	4	5	3	3
13	85	4	4	4	4

APPENDIX B

WEIGHT (GM), LENGTH (MM), AND SEX FOR NEWBORN

SCELOPORUS JARROVI, KITT PEAK, ARIZONA

An. No.	Weight	Snout-Vent	Tail	Sex
1967-1				
a	0.89	30	34	
b	0.81	29	34	
c	0.79	29	35	
d	0.77	29	33	
e	0.71	29	34	
Mean	0.794	29.2	34.0	
1967-2				
a	0.81	28	34	
b	0.81	28	34	
c	0.81	28	34	
d	0.80	29	34	
e	0.78	28	35	
f	0.72	27	32	
g	0.72	29	35	
h	0.71	28	32	
i	0.62	28	34	
Mean	0.753	28.1	33.7	
1967-3				
a	0.78	30	32	
b	0.75	28	12	
Mean	0.765	29.0	--	
1967-4				
a	0.86	29	33	
b	0.82	29	35	
c	0.68	28	33	
Mean	0.786	28.6	33.6	

An. No.	Weight	Snout-Vent	Tail	Sex
1967-5				
a	0.79	28	34	
b	0.78	28	32	
c	0.71	27	33	
Mean	0.760	27.6	33.0	
1967-6				
a	0.82	29	29	
b	0.82	28	33	
c	0.82	28	33	
Mean	0.820	28.3	31.6	
1967-7				
a	0.88	28	32	
b	0.85	28	33	
c	0.84	28	33	
d	0.83	28	31	
e	0.83	27	32	
f	0.81	27	31	
g	0.79	28	22	
h	0.79	28	31	
i	0.74	28	31	
Mean	0.817	27.8	--	
1967-8				
a	0.86	29	36	
b	0.85	28	36	
c	0.82	29	38	
d	0.81	29	35	
e	0.80	29	37	
f	0.80	29	35	
g	0.79	30	37	
h	0.76	28	34	
Mean	0.811	28.8	36.0	

An. No.	Weight	Snout-Vent	Tail	Sex
1967-9				
a	0.76	27	32	
b	0.76	27	32	
c	0.74	27	32	
d	0.74	27	32	
e	0.72	28	32	
f	0.71	27	4	
g	0.71	29	32	
h	0.71	27	32	
i	0.69	27	32	
j	0.68	27	32	
Mean	0.723	27.3	--	
1967-10				
a	0.72	27	32	
b	0.68	26	32	
c	0.67	26	32	
d	0.65	26	31	
Mean	0.680	26.2	31.7	
1967-11				
a	0.86	26	33	
b	0.83	29	35	
c	0.82	28	34	
Mean	0.836	27.6	34.0	
1967-12				
a	0.79	26	31	
b	0.78	28	32	
c	0.77	27	32	
d	0.74	27	31	
e	0.71	26	32	
Mean	0.758	26.8	31.6	
1967-13				
a	0.79	30	31	
b	0.79	28	32	
c	0.78	28	30	
d	0.76	27	32	
e	0.73	27	31	
f	0.73	26	30	

An. No.	Weight	Snout-Vent	Tail	Sex
1967-13				
g	0.72	27	32	
h	0.72	27	30	
i	0.70	27	32	
Mean	0.746	27.3	31.1	
1967-14				
a	0.89	28	32	
b	0.88	27	33	
c	0.88	27	28	
d	0.88	26	31	
e	0.87	27	34	
f	0.87	28	33	
g	0.86	28	33	
h	0.83	27	32	
i	0.82	27	24	
Mean	0.864	27.1	--	
1967-15				
a	0.88	27	30	
b	0.82	27	32	
c	0.81	27	30	
d	0.78	27	32	
e	0.77	28	31	
Mean	0.812	27.2	31.0	
1968-1				
a	0.92	29	35	male
b	0.90	29	35	female
c	0.90	29	36	female
d	0.89	28	35	female
e	0.81	29	33	female
f	0.81	29	34	male
Mean	0.871	28.8	34.6	
1968-2				
a	0.79	28	31	male
b	0.73	27	31	male
c	0.71	28	32	female
Mean	0.743	27.6	31.3	

An. No.	Weight	Snout-Vent	Tail	Sex
1968-3				
a	0.87	29	37	female
b	0.82	28	36	female
c	0.81	28	36	male
Mean	0.833	28.3	36.3	
1968-4				
a	0.83	28	34	male
b	0.80	29	33	male
c	0.79	28	35	male
Mean	0.806	28.3	34.0	
1968-5				
a	0.82	28	33	female
b	0.81	29	24	male
c	0.80	28	33	female
d	0.80	28	33	female
Mean	0.807	28.2	--	
1968-6				
a	0.90	28	34	female
b	0.90	28	33	male
c	0.85	29	33	male
d	0.85	28	33	male
e	0.85	28	33	male
f	0.85	27	32	female
g	0.80	28	34	female
h	0.80	28	32	male
i	0.80	27	34	female
j	0.80	26	33	female
k	0.80	26	32	female
l	0.75	28	32	male
m	0.75	27	32	female
n	0.70	28	22	male
Mean	0.814	27.4	--	
1968-7				
a	0.79	26	21	male
b	0.78	27	32	female
c	0.72	26	32	female
d	0.71	27	29	female
e	0.70	27	33	male

An. No.	Weight	Snout-Vent	Tail	Sex
1968-7				
f	0.70	27	31	female
g	0.70	27	32	male
h	0.70	26	32	female
Mean	0.725	26.6	--	
1968-8				
a	0.83	29	34	male
b	0.82	29	35	male
c	0.78	28	32	male
Mean	0.810	28.6	33.6	
1968-9				
a	0.71	28	28	male
b	0.69	28	32	female
c	0.68	28	28	male
Mean	0.690	28.0	29.3	
1968-10				
a	0.92	29	21	male
b	0.82	29	34	female
c	0.78	28	35	male
d	0.68	29	34	female
Mean	0.800	28.7	--	
1969-1				
a	0.92	30	33	male
b	0.92	28	33	female
c	0.92	27	33	male
d	0.87	28	32	male
e	0.84	29	33	female
f	0.83	29	35	male
g	0.82	27	33	female
h	0.81	29	35	female
i	0.78	28	27	female
j	0.70	27	35	female
Mean	0.841	28.2	32.9	
1969-2				
a	0.92	29	31	female
b	0.90	29	34	male
c	0.82	27	33	female
Mean	0.880	28.3	32.6	

An. No.	Weight	Snout-Vent	Tail	Sex
1969-3				
a	0.92	29	30	female
b	0.85	28	33	female
c	0.81	29	35	male
d	0.81	29	33	male
e	0.79	29	34	female
Mean	0.836	28.8	33.0	
1969-4				
a	0.98	30	34	male
b	0.82	29	35	male
c	0.82	28	30	male
d	0.81	29	35	female
e	0.79	29	36	male
f	0.79	28	33	female
g	0.79	27	32	female
h	0.78	29	33	female
i	0.78	27	34	female
Mean	0.817	28.4	33.5	
1969-5				
a	1.02	30	36	male
b	0.93	30	36	female
c	0.89	29	37	female
d	0.88	28	36	female
e	0.83	29	36	male
f	0.83	28	37	female
g	0.71	27	35	female
Mean	0.870	28.7	36.1	
1969-6				
a	0.80	28	34	male
b	0.78	27	32	male
c	0.77	28	33	male
d	0.72	28	30	male
e	0.72	27	32	female
f	0.69	28	34	male
Mean	0.746	27.6	32.5	
1969-7				
a	0.78	29	36	male
b	0.78	28	36	male
c	0.77	28	35	female
Mean	0.776	28.3	35.6	

An. No.	Weight	Snout-Vent	Tail	Sex
1969-8				
a	0.86	28	34	female
b	0.86	28	33	female
c	0.82	28	34	male
d	0,82	28	33	male
e	0.81	29	35	female
f	0.81	29	34	female
g	0.79	28	32	male
h	0.78	27	31	male
i	0.71	28	33	female
Mean	0.806	28.1	33.2	
1969-9				
a	0.81	29	18	male
b	0.81	28	34	male
c	0.80	29	33	female
d	0.80	28	33	female
e	0.80	26	33	female
f	0.77	28	36	male
g	0.76	28	34	female
h	0.71	28	34	male
Mean	0.782	28.0	--	
1969-10				
a	0.81	29	35	male
b	0.81	29	34	female
c	0.80	30	35	female
d	0.80	28	33	female
e	0.80	28	33	male
f	0.78	29	34	female
g	0.78	29	33	male
h	0.76	29	34	female
Mean	0.792	28.8	33.8	
1969-11				
a	0.83	28	34	male
b	0.82	27	14	female
c	0.79	27	34	female
d	0.78	29	11	male
e	0.78	27	35	female
f	0.72	29	34	female
g	0.72	28	35	female
Mean	0.777	27.8	--	

An. No.	Weight	Snout-Vent	Tail	Sex
1969-12				
a	0.94	29	36	male
b	0.91	30	34	female
c	0.91	29	34	female
d	0.88	30	35	female
e	0.88	30	35	male
f	0.88	29	35	male
g	0.87	29	35	female
h	0.82	28	13	male
i	0.81	28	35	female
j	0.80	29	34	female
Mean	0.870	29.1	--	

APPENDIX C

MATERNAL WEIGHT LOSS DURING PARTURITION IN

SCELOPORUS JARROVI, KITT PEAK, ARIZONA

An. No.	Field Weight	Weight after Parturition	% Weight Loss
1967-1	12.51	7.77	37.8
1967-2	25.65	13.10	48.9
1967-3	11.04	7.10	35.6
1967-4	9.72	6.04	37.8
1967-5	9.62	6.31	34.4
1967-6	10.71	6.79	36.6
1967-7	26.52	15.02	43.3
1967-8	24.59	15.03	38.8
1967-9	27.46	16.13	41.2
1967-10	10.78	6.77	37.1
1967-11	11.58	7.62	34.1
1967-12	12.15	7.13	41.3
1967-13	20.78	11.50	44.6
1967-14	23.20	13.58	41.4
1967-15	24.32	15.14	37.7

An. No.	Field Weight	Weight after Parturition	% Weight Loss
1968-1	17.17	10.72	37.5
1968-2	10.42	7.18	31.0
1968-3	11.18	9.25	17.2
1968-4	9.88	5.76	41.7
1968-5	12.82	7.70	39.9
1968-6	29.20	18.20	39.1
1968-7	20.98	13.50	35.6
1968-8	9.46	7.11	24.8
1968-9	20.41	15.61	23.5
1968-10	12.83	8.79	31.4
1969-1	26.61	17.62	33.7
1969-2	12.32	8.40	31.8
1969-3	18.31	14.13	22.8
1969-4	21.93	15.12	31.0
1969-5	25.30	16.13	36.2
1969-6	14.27	9.68	32.1
1969-7	8.72	6.59	24.4
1969-8	22.70	15.68	30.9
1969-9	22.40	14.38	35.8

An. No.	Field Weight	Weight after Parturition	% Weight Loss
1969-10	23.98	14.02	41.5
1969-11	16.70	11.17	31.2
1969-12	25.23	14.72	41.6

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