

SEASONAL ALTERATIONS IN THE ADRENAL, THYROID, AND
GONADS OF NORMAL AND ADRENAL MANIPULATED
PIGEONS, COLUMBA LIVIA

It was Riddle (1923) who for the first time noted (1) increased adrenal weight preceeding and during ovulation in the pigeons thereby suggesting a parallel adrenal-gonad axis. Later findings on many other species of birds gave substantial validity to the concept of parallel adrenal-gonad axis (Legait and Legait, 1959; Fromme Bouman, 1962; Lorenzen and Farner 1964; Höhn et al., 1965). Subsequently, studies of soule and Assenmacher (1966), Assenmacher and Boissin (1970) and Bengt (1979) have also brought out an antagonistic relationship between adrenals and gonads of certain other species of birds. This antagonistic inter-relationship between testicular and adrenal secretions was further emphasized by the observed alterations in plasma corticosterone in castrated and testosterone treated ducks (Daniel and Assenmacher, 1969).

Reports highlighting the inter-relationship between adrenal and gonads of lower vertebrates are also available. Parallel qualitative and quantitative changes occurring in the interrenal tissue and gonads of the male Puntius sophore and of the air breathing fish, H. Fossilis have been

reported by Nalini and Dixit(1976) and Munshi et al.(1978) based on their seasonal histological studies. The only report available on this line in the case of amphibians is that of Srivatsava et al.(1984) indicating a negative influence of exogenously administered Deoxy-corticosterone on spermatogenesis and steroidogenesis in the testis of ^{the} frog, R.tigrina. Investigations involving seasonal variations in adrenal activity in relation to reproductive functions in reptiles are scanty and few reports suggest increased adrenocortical functioning during the sexual activity (Gabe,1970).

However, Daughtery and Callard (1972) reported that there was no tendency for the corticosteroid level to vary with the reproductive cycle. Apparently, the reports reviewed above suggest influence of adrenal steroids on gonadal physiology varying from indifferent to synergistic to antagonistic ones in the various sub-mammalian species..

Seasonal morphological alterations involving the thyroid gland have also been recorded. For quite some time, number of converging investigations had demonstrated pronounced beneficial effects of thyroid hormones on gonadal functioning in domestic species of birds (Woitkewitch,1940; Wheeler et al., 1948; Shaffner and Andrews, 1948; Kumaran and Turner, 1949;

Thapliyal and Garg, 1969). Intensive investigations on several species of subtropical Indian finches further led to the establishment of distinct synergistic and antagonistic relationships between thyroid and gonads (Pandha and Thapliyal, 1964; Thapliyal and Pandha, 1965, 1967 a,b; Thapliyal and Bagheshwar, 1970; Chandola, 1972). A categorisation seems to indicate the domestic species of birds to belong to the parallel thyroid-gonad axis group (Chaturvedi and Thapliyal, 1980; Thapliyal et al., 1982) and the wild forms to the inverse thyroid-gonad axis group (Riddle, 1925; Thapliyal and Pandha, 1967 a,b; Jallageas and Assenmacher, 1974; Chandola and Thapliyal, 1974; Jallageas et al., 1978).

Previous studies from this laboratory on wild and domestic pigeons had revealed parallel adrenal-gonad relationship in both, and inverse thyroid-gonad relationship in the former and parallel thyroid-gonad axis in the latter (Patel et al., 1985; Ramachandran et al., 1987; Ramachandran and Patel, 1986), findings which are in agreement with the categorisation made above. It was in this context that a detailed investigation on adrenal, thyroid and gonads of Feral blue rock pigeons, Columba livia have been studied on a seasonal basis in both normal as well as adrenal manipulated birds.

MATERIALS AND METHODS
As Outlined in Chapter I
OBSERVATIONS

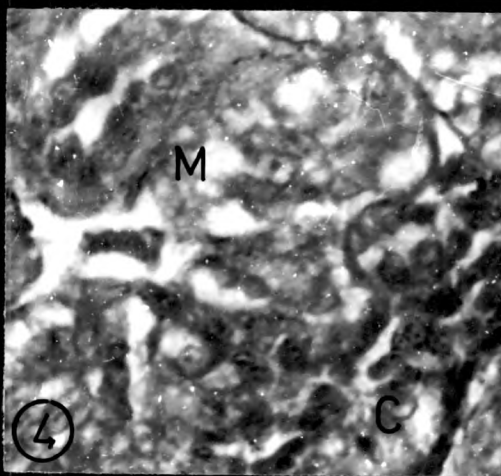
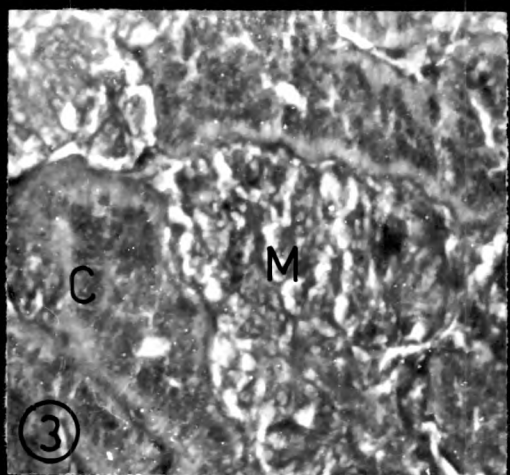
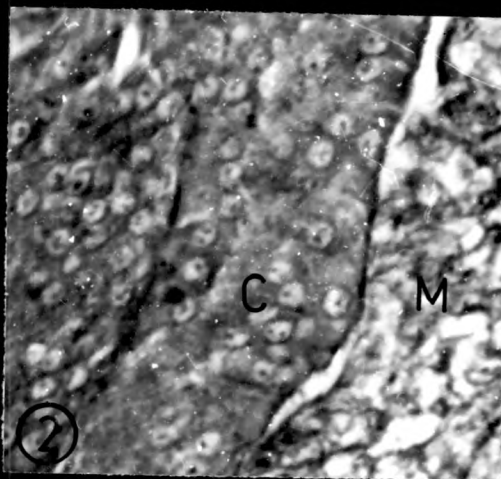
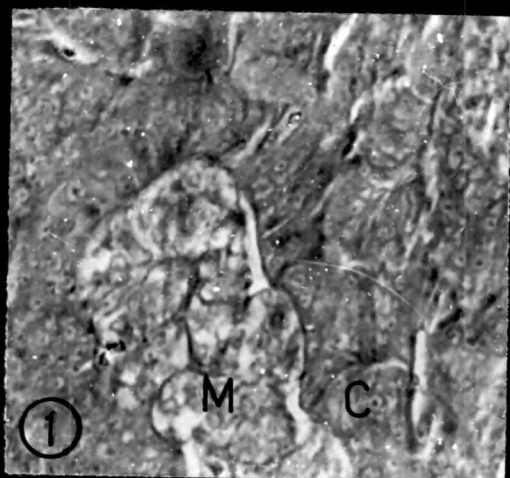
Adrenal

Normal birds exhibited distinct histological alterations in adrenal structure in relation to annual gonadal cyclicity. During the recrudescence and breeding periods, the adrenal was marked by increased cortico-medullary ratio with prominent cortical strands consisting of enlarged interrenal cells with prominent nuclei (figs. 1, 2, 9 and 10). The cortex to medulla ratio was 3:1 during the recrudescence period which got further increased to 6:1 during the breeding period. During the regression period, the cortico-medullary ratio decreased to 3:2 and was histologically marked by decreased size of cortical strands with regressed interrenal cells (figs. 17 and 18).

Dxm treatment with all three dose regimens during the recrudescence and breeding months brought about noticeable suppressible effect on the corticomedullary ratio. Whereas the average ratio during the recrudescence period was 2:1, that during the breeding period got reduced to 1:1. The cortical cells were also regressed and presented a picture

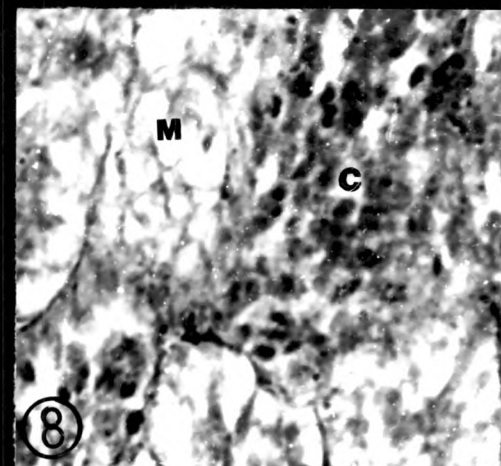
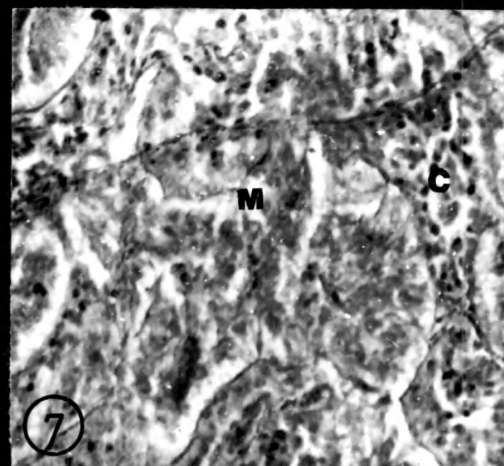
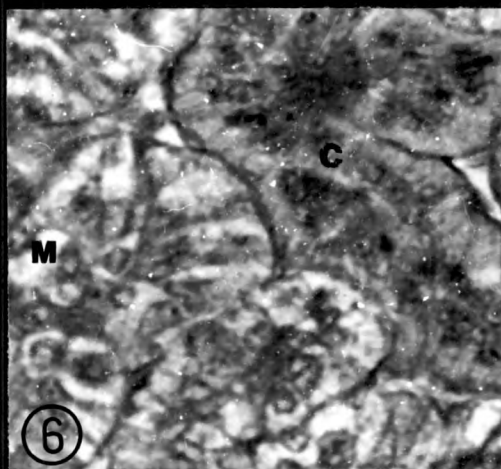
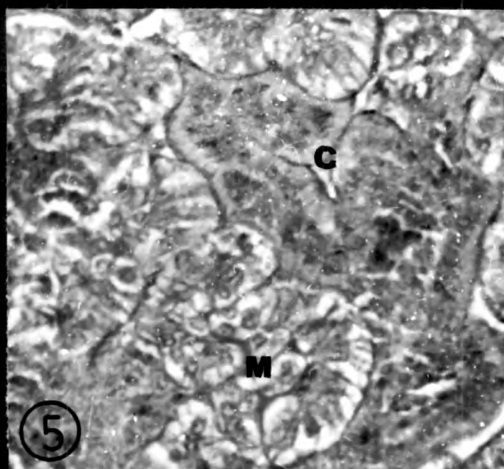
EXPLANATION TO FIGURES.

- Fig. 1 - Photomicrograph of the adrenal of normal birds ^{during} recrudescence showing prominent cortical strand(c) 200x.
M - Medulla.
- Fig. 2 - Enlarged version of the same. 400x.
- Fig. 3 - Photomicrograph of the adrenal treated with 80 μ g 4xm during recrudescence. 200x. Note the clear out regression of the cortical strand(c).
- Fig. 4 - Enlarged version of the same. 400x.



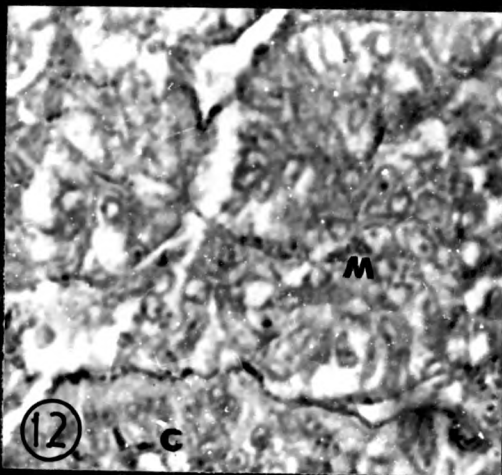
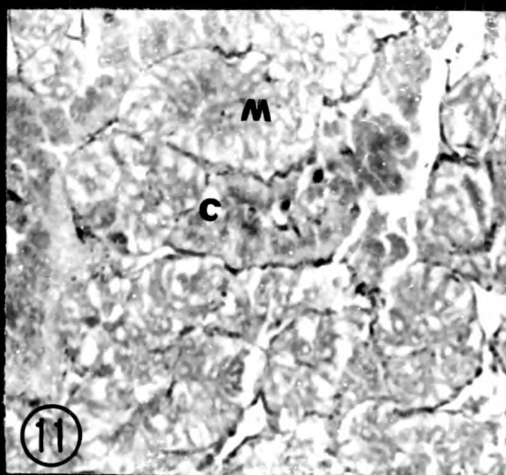
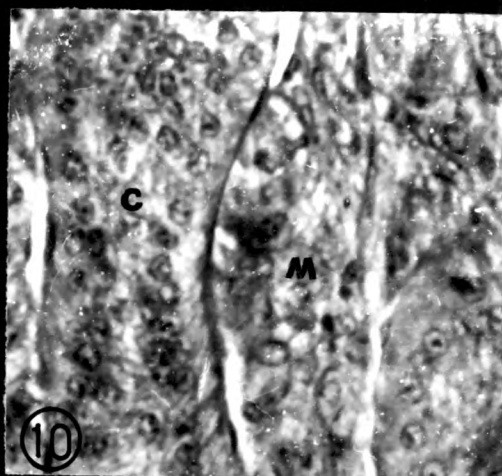
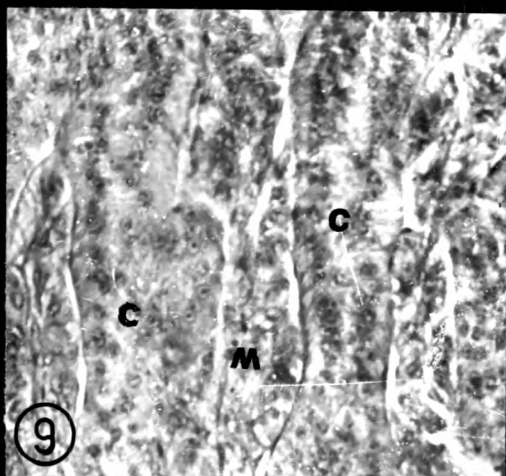
EXPLANATION TO FIGURES.

- Fig. 5 - Photomicrograph of the adrenal treated with 120 μ g dxm during recrudescence. 200x. Note the cortical(c) regression less pronounced than in fig.3. M \rightarrow Medulla.
- Fig. 6 - Enlarged version of the same. 400x.
- Fig. 7 - 160 μ g dxm treated adrenal during recrudescence showing pronounced cortical (c) regression. 200x.
- Fig. 8 - Enlarged version of the same. 400x.



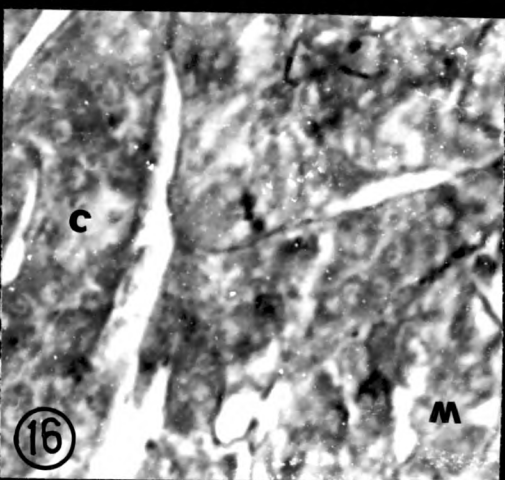
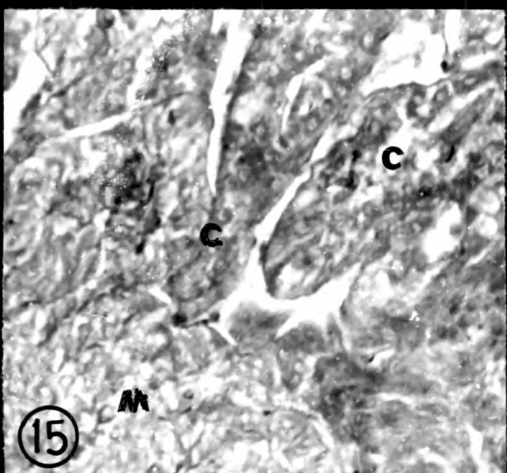
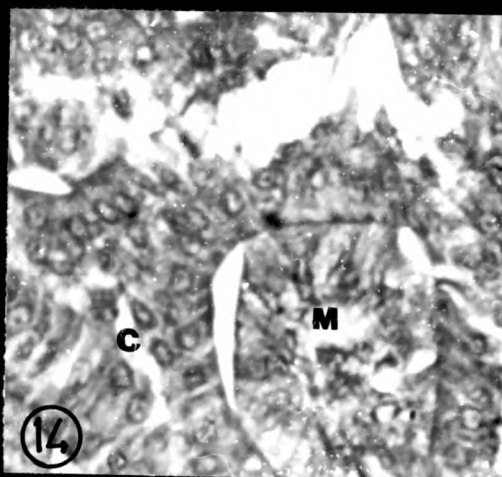
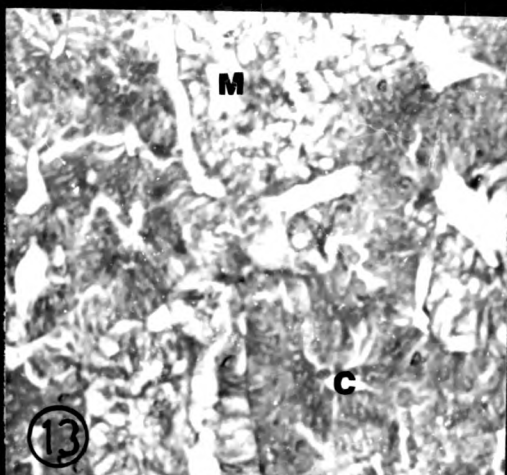
EXPLANATION TO FIGURES.

- Fig. 9 - Photomicrograph of the adrenal of normal birds during breeding. 200x. Note the extensive cortical(c) development. M - Medulla.
- Fig. 10 - Enlarged version of the same. 400x.
- Fig. 11 - 80 μ g dxm treated adrenal during breeding. 200x. Note the highly regressed cortex (c).
- Fig. 12 - Enlarged version of the same. 400x.



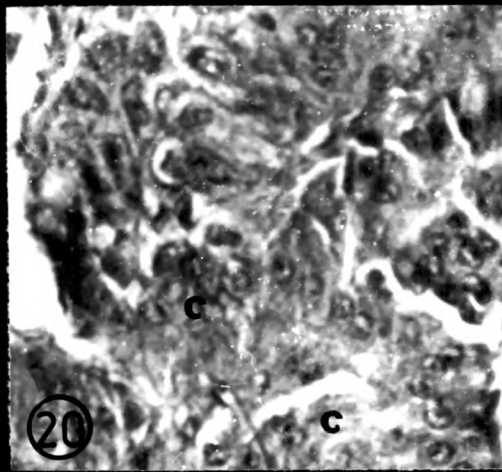
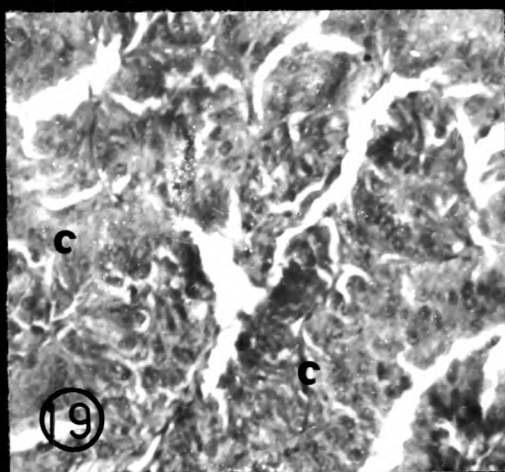
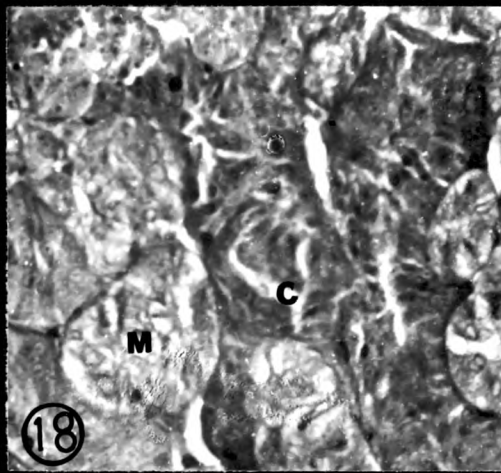
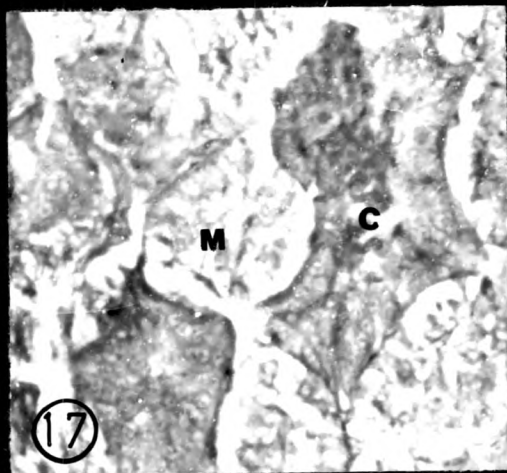
EXPLANATION TO FIGURES

- Fig. 13 - Photomicrograph of 120 μ g dxm treated adrenal during breeding. 200x. Note the marked cortical (c) regression. M - Medulla.
- Fig. 14 - Enlarged version of the same. 400x.
- Fig. 15 - 160 μ g dxm treated adrenal during breeding showing cortical (c) regression and disruption. 200x.
- Fig. 16 - Enlarged version of the same. 400x.



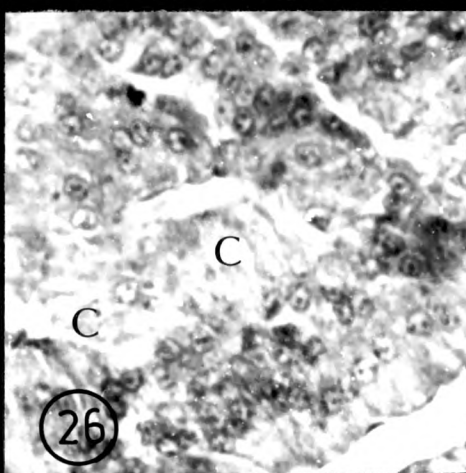
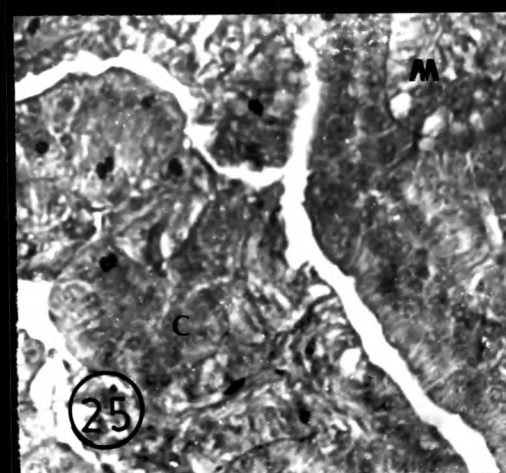
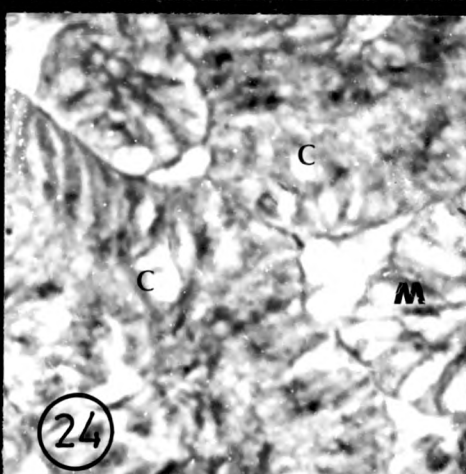
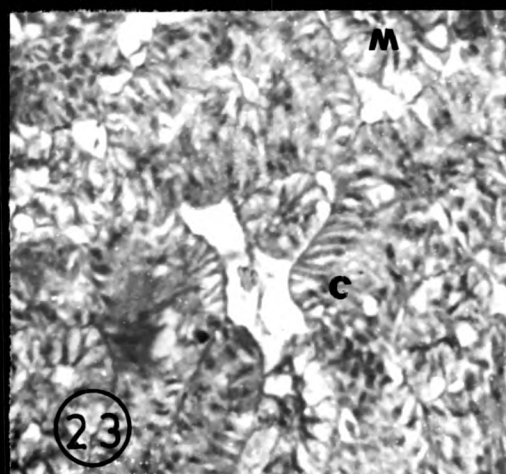
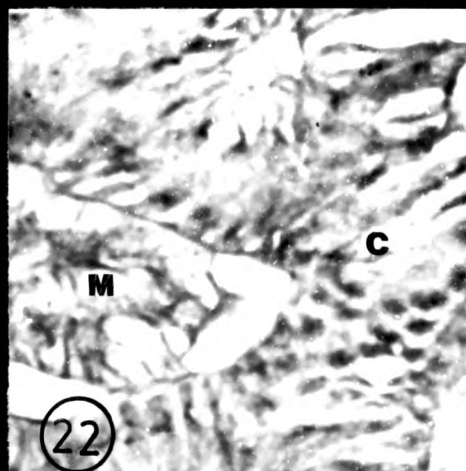
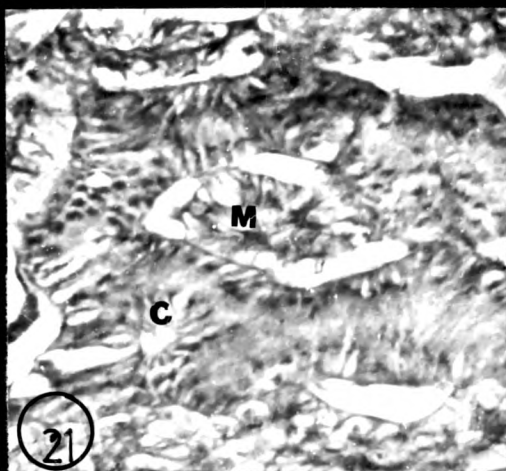
EXPLANATION TO FIGURES.

- Fig. 17 - Photomicrograph of the adrenal of normal birds during regression. 200x.
Note the regressed cortex (c). M - Medulla.
- Fig. 18 - Enlarged version of the same. 400x.
- Fig. 19 - ACTH treated adrenal during regression showing cortical(c) enlargement. 200x.
- Fig. 20 - Enlarged version of the same. 400x.



EXPLANATION TO FIGURES.

- Fig. 21 - Photomicrograph of the adrenal treated with low corticosterone dose in *the* morning during regression 200x. Marked cortical (c) enlargement is visible.
M - Medulla.
- Fig. 22 - Enlarged version of the same. 400x.
- Fig. 23. - Adrenal treated with low corticosterone dose in the evening during regression. 200x. Note the cortical (c) activation.
- Fig. 24 - Enlarged version of the same. 400x.
- Fig. 25 - Adrenal treated with high corticosterone dose in the morning during regression showing cortical (c) activation. 200x.
- Fig. 26 - Enlarged version of the same. 400x.



comparable to the control birds during the regression phase (figs. 3, 4, 5, 6, 7, 8, 11, 12, 13, 14, 15 and 16). ACTH and corticosterone administrations during the regression period induced adrenal activation marked by enlarged cortical strands and increased cortico-medullary ratio of 3:1. This alteration was common for all corticosterone doses as well as for ACTH (figs. 19-26).

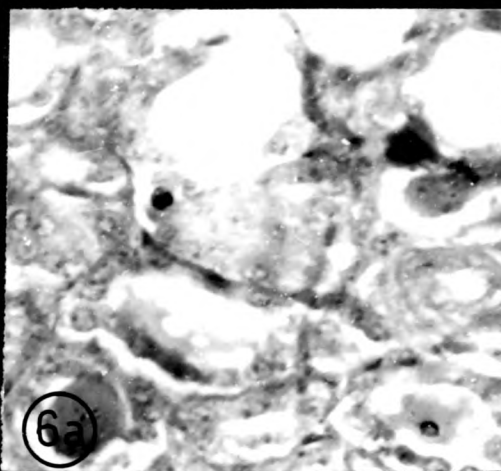
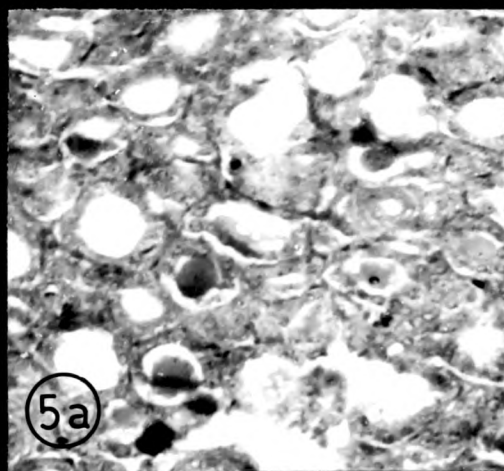
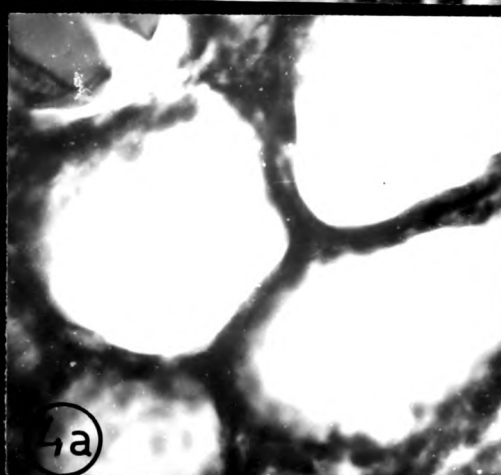
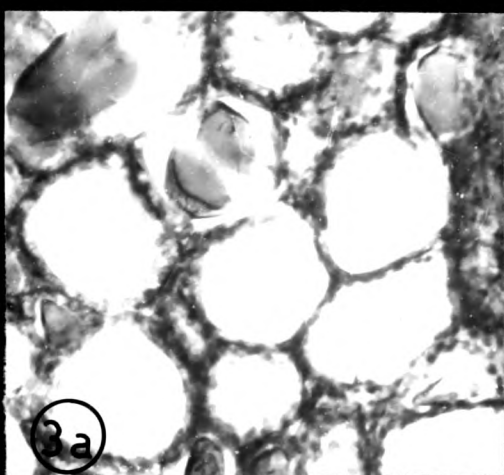
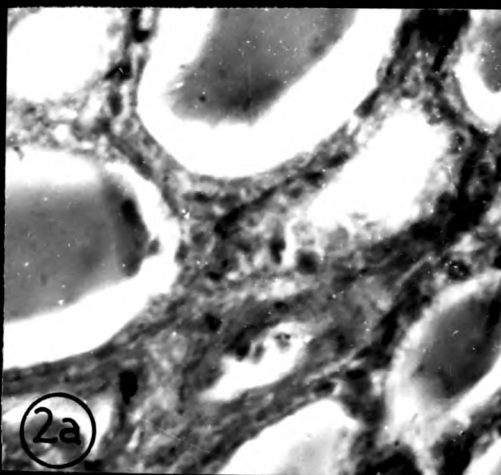
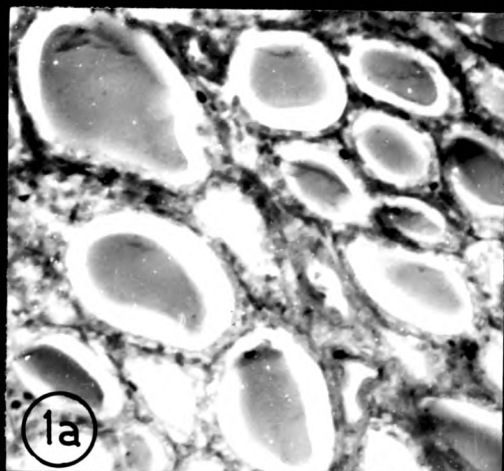
Thyroid

The thyroid of normal birds during ^{the}recrudescent period showed follicles in size ranging from small to medium to large with varying amounts of colloid. Follicular epithelium was cuboidal, and the general appearance indicated decreased colloid release coupled with reduced functioning (figs. 1a and 2a). However, the breeding period was marked by increased cell height of the follicles and slightly decreased colloidal content (fig. 7a). The thyroid in the regression phase exhibited maximal cell height with depleted colloidal content. A few follicles tended to show presence of freshly synthesised colloid (figs. 11a and 12a).

Dxm treated birds during recrudescence revealed a relatively more active state of the gland. Though the cell height was not altered, the loss of colloid was clearly

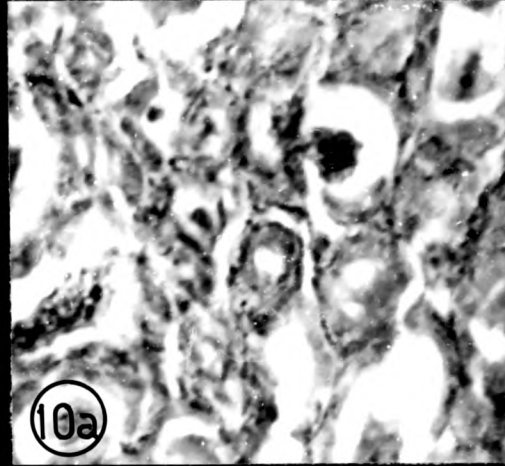
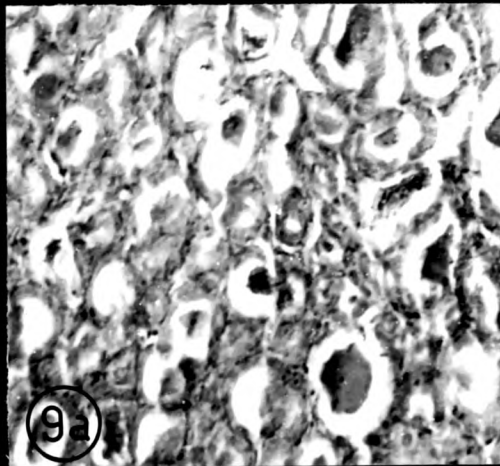
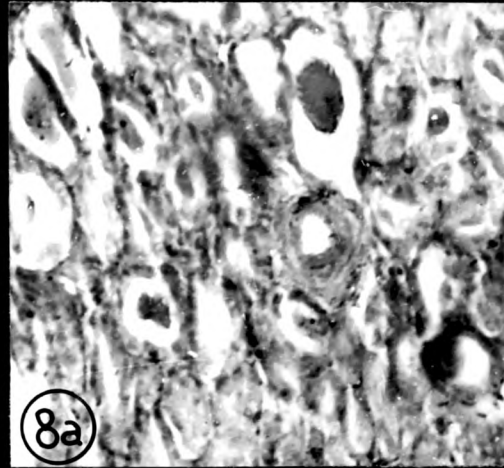
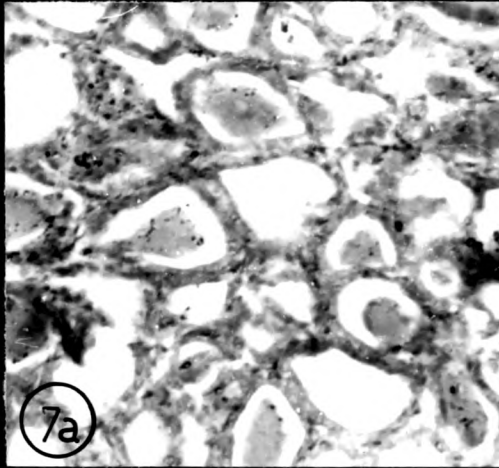
EXPLANATION TO FIGURES.

- Fig. 1a - Photomicrograph of thyroid of normal birds during recrudescence showing follicles of varying sizes. 200x.
- Fig. 2a - Enlarged version of the same. 400x.
Note the cuboidal epithelium.
- Fig. 3a - Thyroid of birds treated with 120 μ g dxm during recrudescence. 200x.
Note the empty follicles.
- Fig. 4a - Enlarged version of the same. 400x.
- Fig. 5a - Thyroid of birds treated with 160 μ g dxm during recrudescence. 200x. Note the absence of colloid in many follicles and regressed follicles.
- Fig. 6a. - . Enlarged version of the same. 400x.



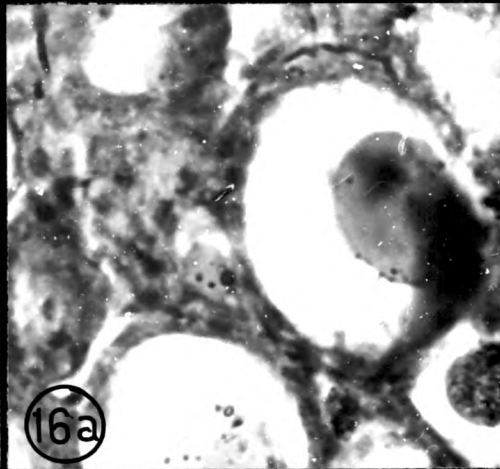
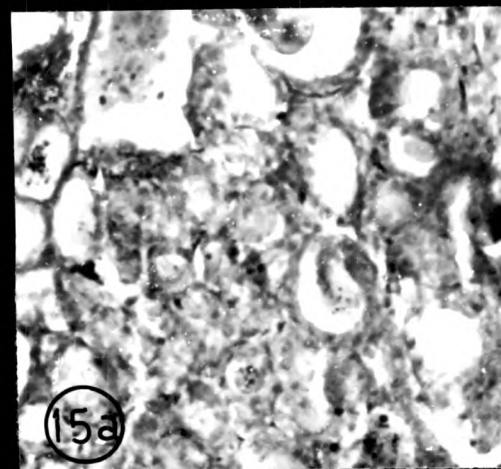
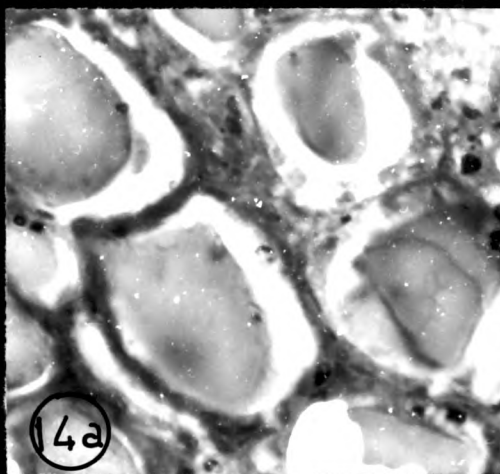
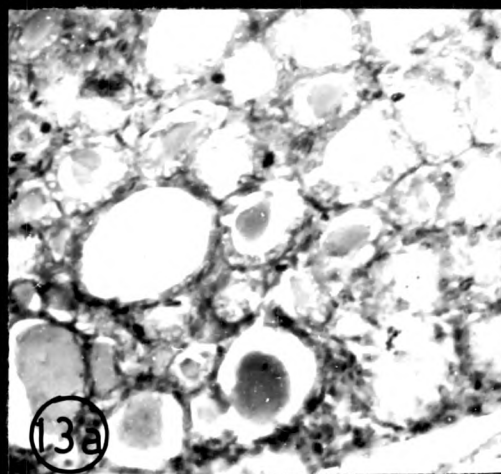
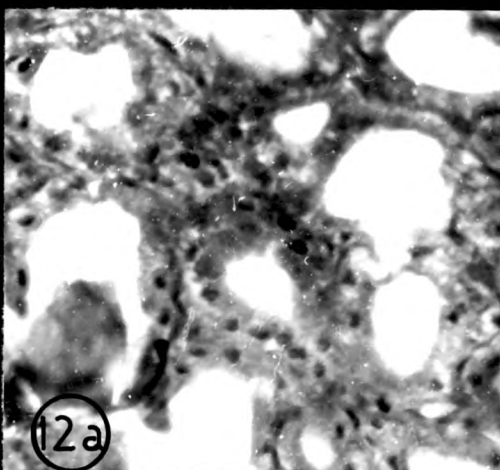
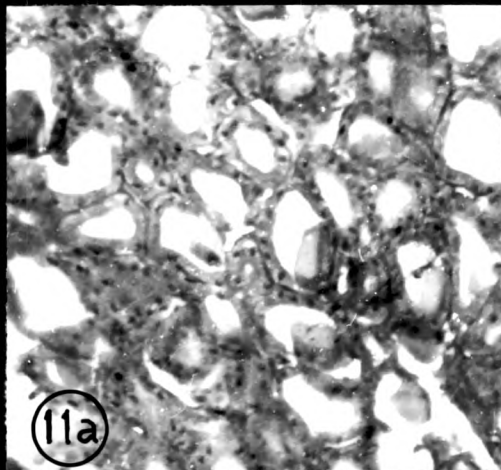
EXPLANATION TO FIGURES

- Fig. 7a - Photomicrograph of thyroid of normal birds during breeding showing loss of colloid from some follicles. 200X.
- Fig. 8a - Thyroid of birds treated with $120\mu\text{g}_L^{dxm}$ during breeding showing marked reduction in size of *the* follicles and absence of colloid. 200X
- Fig. 9a - Thyroid of birds treated with $160\mu\text{g}_L^{dxm}$ during breeding showing reduced size of follicles, absence of colloid and signs of follicular disruption. 200X.
- Fig. 10a - Enlarged version of the same.



EXPLANATION OF FIGURES.

- Fig. 11a - Photomicrograph of thyroid of normal birds during regression showing reduced size of the follicles with prominent epithelium and depleted collidal content 200x.
- Fig. 12a - Enlarged version of the same.
- Fig. 13a - ACTH treated thyroid during regression. 200x. Note the enlarged follicles, cuboidal epithelium and increased colloidal content.
- Fig. 14a - Enlarged version of the same. 400 X.
- Fig. 15a - Thyroid treated with low corticosterone morning dose. 200x.
- Fig. 16a - Thyroid treated with low corticosterone evening dose. 200x.



evident. The effect of all three dose regimens of dxm were more or less similar though the highest dose tended to include visible follicular damage (figs. 3a and 4a). Dxm treatment during the breeding phase resulted in similar set of changes as that of recrudescence (figs. 8a to 10a). ACTH administration during the regression phase showed prominent follicles with cuboidal epithelium exhibiting more colloid content (figs. 13a and 14a). LCM and LCE treatment brought about increased cell height with hypertrophied appearance and depleted colloidal content in many of the follicles (figs. 15a and 16a). HCM and HCE increased the cell height and reduced the follicular size; and varying content of colloid could be seen in the follicles.

Testis

Recrudescent and breeding phases were marked by enlarged seminiferous tubules exhibiting active spermatogenesis. Whereas during the recrudescence period the tubules depicted spermatogonia, spermatocytes and spermatids appearance of sperms was evidenced only during the breeding phase (figs. 1c, 2c and 7c). Interstitium was well formed exhibiting normal activity. The regression phase was marked by thickened basal membrane and regressed tubules with

hypertrophied spermatogonial cells. Most of the other cell types were more less degenerated and appeared as large vacuolated cells with prominent pycnotic nuclei. Clumps of chromatin material could also be observed. Interstitium was flattened indicating reduced functional competence (Figs. 11c and 12c).

Although dxm treatment in general resulted in degenerative changes, the degree of degeneration varied with the dose regimens. Reduction in tubular diameter was closely related to the dosage, with 80µg showing minimum reduction and 160µg showing maximum reduction. Other histological features visible were thickened basement membrane and flattened inactive interstitium. 80µg dxm depicted maximum tubular damage marked by total cellular degeneration of more mature cells of the germinal epithelium (spermatocytes, spermatids and spermatozoa) leading to an accumulation of cell debris in the lumen of the shrunken tubules. The spermatogonial cells were however hypertrophied and many of them showed rampant nuclear pycnosis (Fig. 3c). The 160µg treatment depicted all the above changes accompanied by more advanced degenerative and necrotic changes, while 120µg showed less severe damages (Figs. 4c to 6c). Dxm treatment during the breeding season brought about more prominent degenerative changes as compared to the recrudescence phase. 80µg treatment resulted in total degeneration with a fibrous appearance.

EXPLANATION TO FIGURES.

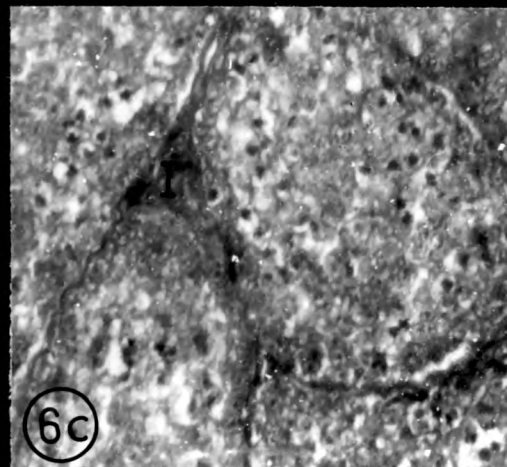
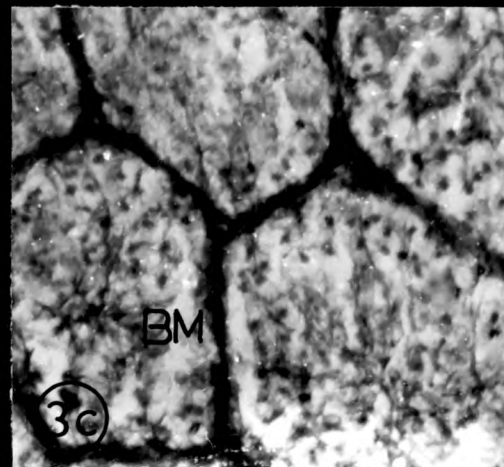
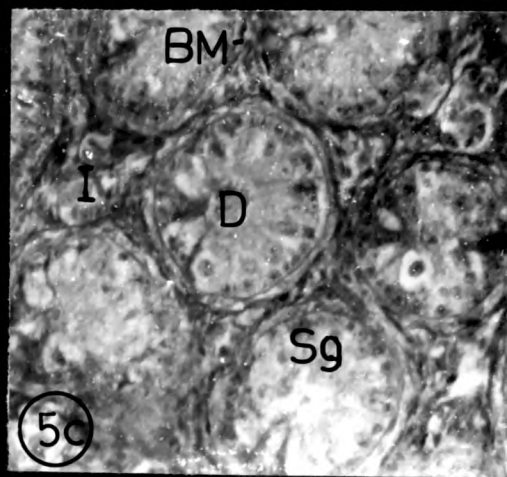
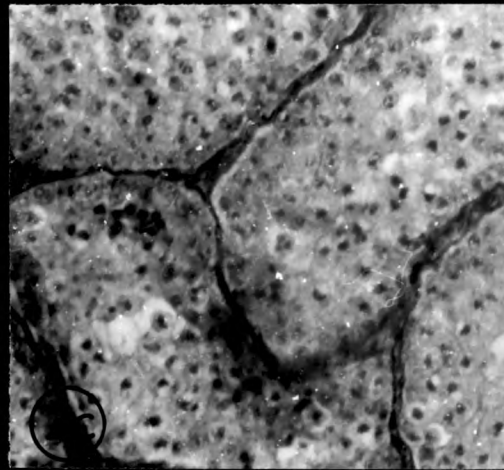
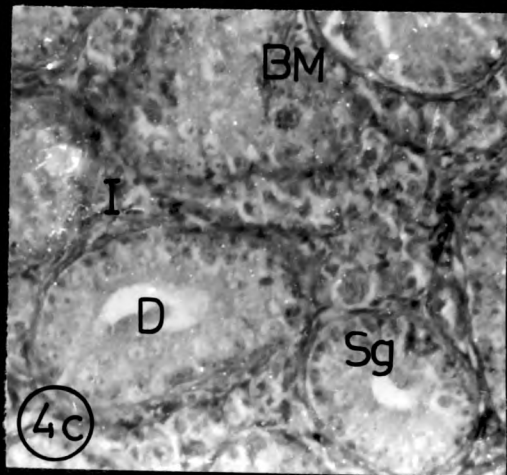
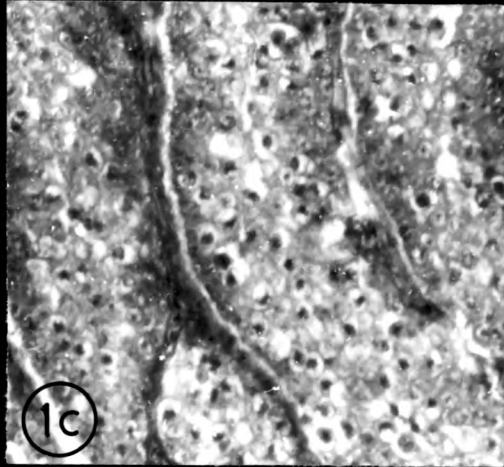
Figs. 1c & 2c - Photomicrographs of the testis of normal birds during recrudescence showing well formed seminiferous tubules with active germinal epithelium. 200x.

Fig. 3c. - Testis of birds treated with 80 μ g dxm during recrudescence. 200x.
Note the reduced tubules, thickened basement membrane and degenerated germinal epithelium. BM - Basement membrane.

Fig. 4c & 5c - Testis of birds treated with 120 μ g dxm during recrudescence showing regressed tubules with thickened basement membrane, hypertrophied spermatogonia and debris in the lumen. 200x. BM - Basement Membrane. D- Debris

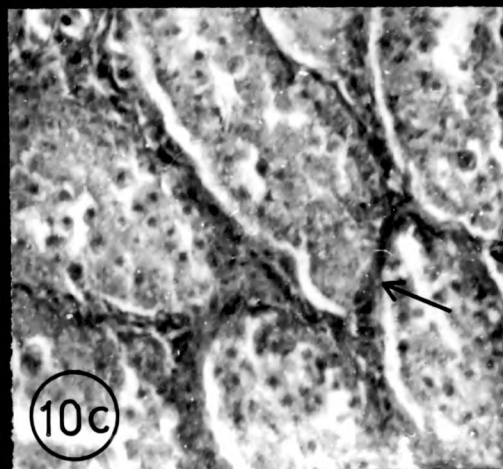
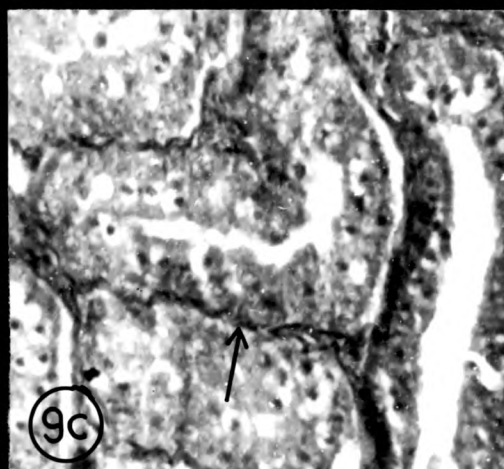
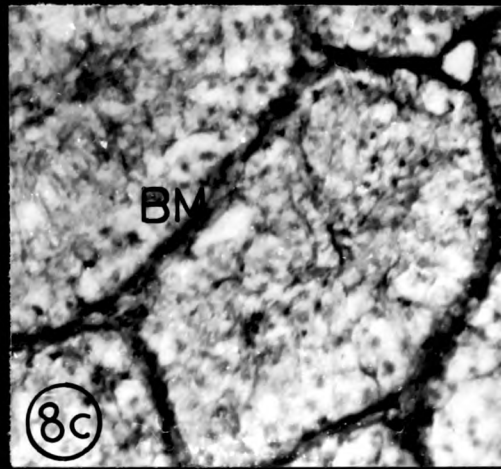
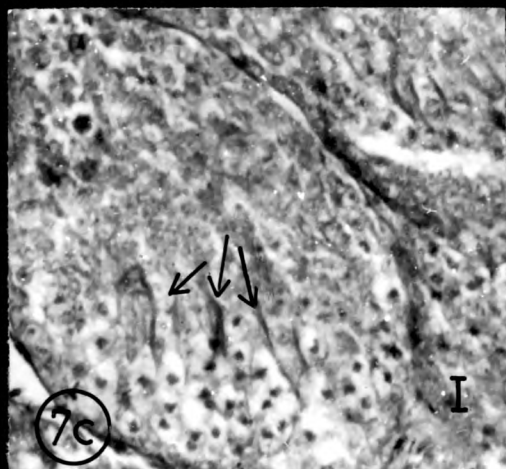
I - Interstitium Sg- Spermatogonia

Fig. 6c - Testis of birds treated with 160 μ g dxm during recrudescence showing degenerating germ cells and regressing interstitium(I). 200x.



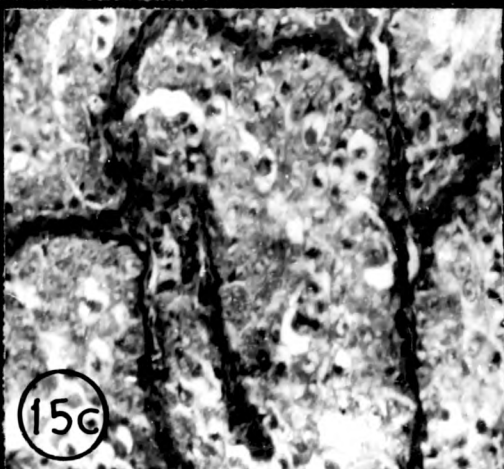
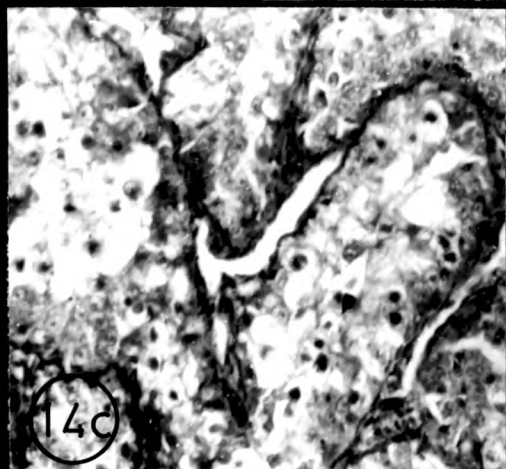
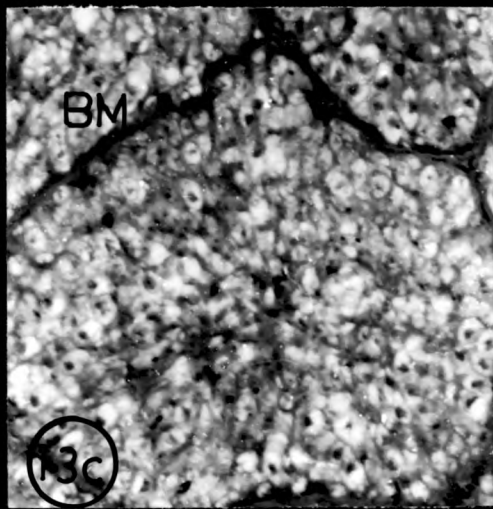
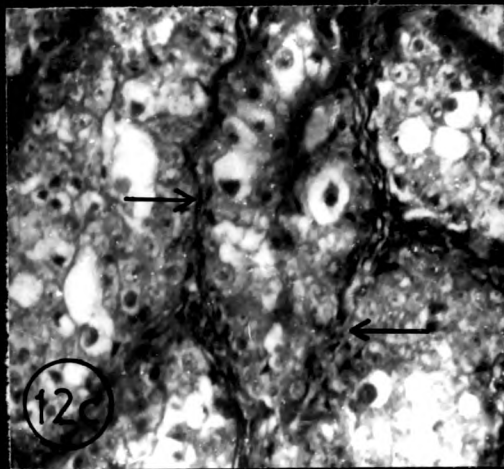
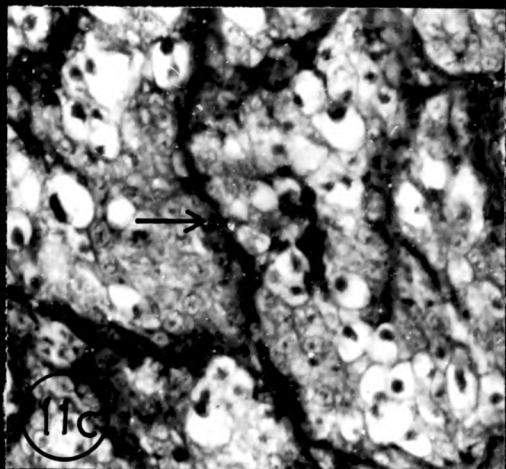
EXPLANATION TO FIGURES

- Fig. 7c - Photomicrograph of the testis of normal birds during breeding. 200X. Note the appearance of spermatozoa (arrows) I - Interstitium.
- Fig. 8c - Testis of birds treated with 80 μ g dxm during breeding showing reduced tubules with thickened basement membrane and degenerating germinal epithelium. 200X. BM - Basement membrane.
- Fig 9c - Testis of birds treated with 120 μ g dxm during breeding. 200X. Note the more regressed nature of the tubules, irregular basement membrane (arrow) and degenerating germ cells.
- Fig. 10c - Testis of birds treated with 160 μ g dxm during breeding showing reduced tubular size with thickened and irregular basement membrane (arrows) and germ cell degeneration. 200X.



EXPLANATION TO FIGURES

- Figs. 11c & 12c - Photomicrographs of testis of normal birds during regression. 200X. Note the thickened irregular basement membrane (arrows), regressed tubules and vacuolated appearance of the degenerating germ cells.
- Fig. 13c. - Testis of birds treated with ACTH during regression showing tubular enlargement, less thick basement membrane and reversal of degenerative changes. 200X. BM - Basement membrane.
- Figs. 14c & 15c - Testis of birds treated with low corticosterone morning dose during regression. 200X. Note the recovery of germinal epithelium.

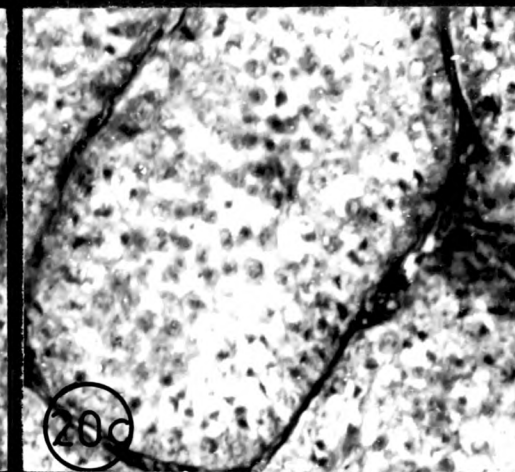
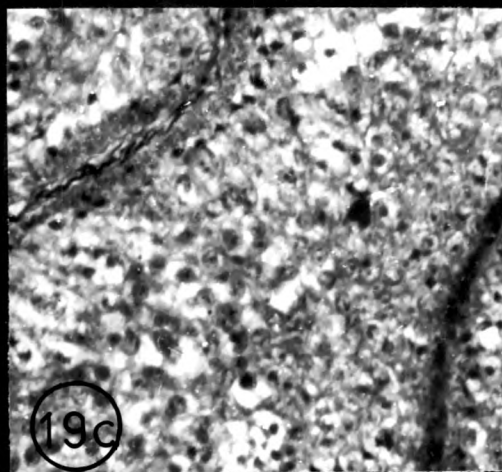
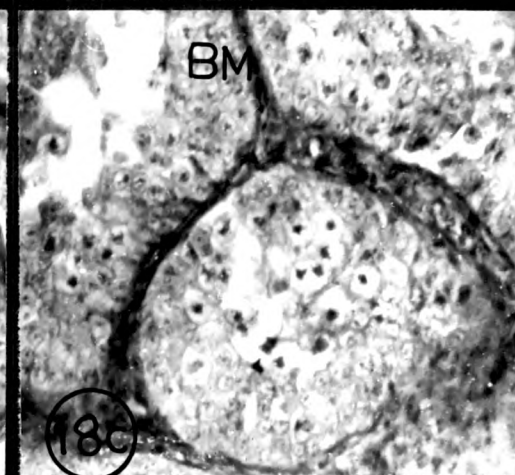
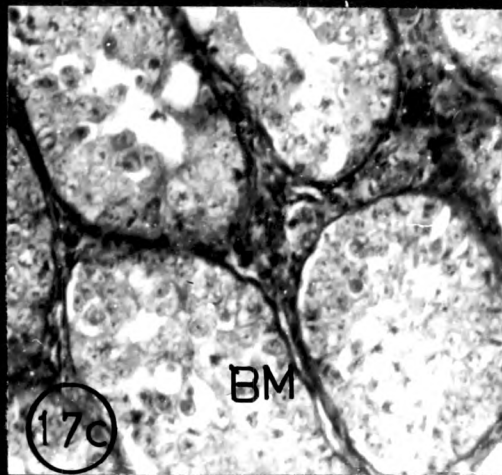
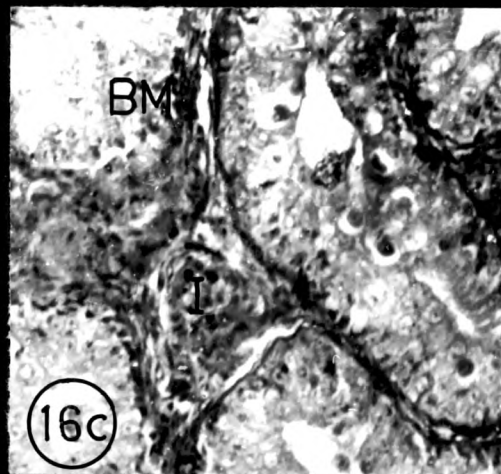


EXPLANATION TO FIGURES

Fig. 16c - Photomicrograph of the testis of pigeon treated with low corticosterone dose in the evening during regression showing small size of the tubule with recovering germinal epithelium. 200X. Note the thinner basement membrane (BM) and recovering interstitium(I).

Figs. 17c
& 18c - Testis of pigeons treated with high corticosterone morning dose during regression. 200X. Basement membranes (BM) are still thick. Size of the tubules are small and germ cell recovery evident.

Figs. 19c
& 20c - Testis of pigeon treated with high corticosterone evening dose during regression. 200X. Note the enlarged tubules with less pronounced recovery of germ cells.



Likewise, 120 μ g resulted in more prominent damage depicting cytolysis and nuclear pycnosis. 160 μ g treatment gave a hypertrophied appearance accompanying ^{the} degenerative changes. Nuclear pycnosis was very prominent (figs. 8c to 10c). ACTH administration induced enlargement of tubular diameter though the basement membrane was still thicker. Though many of the tubules showed large vacuolated cells, some of the tubules showed signs of recovery to varying degrees. However the interstitium appeared still regressed (fig. 13c). LCM treatment brought about tubular enlargement to varying degrees. Even the basement membrane of some tubules exhibited reduced thickness. Ameliorative changes in the germinal cells were more pronounced than that seen with ACTH treatment. Recovery of germinal epithelium was marked by the presence of many spermatogonia with functional nuclei. However the degree of recovery was poor in the other cell types (figs. 14c and 15c). LCE treatment showed less effects of recovery and the histological appearance of testis was more like that of 120 μ g dxm treated birds. Tubular enlargement was also not that prominent and moreover the interstitium remained regressed (fig. 16c). HCM also exhibited some recovery changes with some tubules tending to show enlargement. Many germinal cells were vacuolated with persisting nuclear damage depicting clumped chromatin material. The basement membrane was also

thick (fig. 17c and 18c). Similarly, HCE treatment also showed some signs of recovery in the form of enlargement of some tubules. However most of the degenerative changes were still persistent (figs. 19c and 20c).

Ovary

The ovary in the recrudescence phase depicted many follicles at various stages of development. The pre-ovulatory follicles showed well differentiated thecal and granulosa layers (figs. 1d and 2d). Breeding phase was marked by mostly medium to large sized follicles with few post-ovulatory follicles. Mature follicles showed extensive thecal development with clear differentiation of theca interna and externa and well formed granulosa. The stromal tissue in general exhibited acidophilia (figs. 8d to 10d). In contrast, the regression phase denoted degenerative changes affecting both stromal tissue and follicles. Unovulated follicles exhibited complete regression of granulosa with indistinguishable thecal layers. The stromal tissue exhibited reduced acidophilia (figs. 17d to 18 d).

Dxm treatment during recrudescence rendered visible degenerative changes in the follicles marked by nuclear pycnosis. The stromal tissue depicted marked basophilia. 120µg dxm treatment revealed a generalised damaging influence with many developing follicles depicting degenerative changes

EXPLANATION TO FIGURES.

Fig. 1d - Photomicrograph of the ovary of normal pigeon during recrudescence showing follicles in various stages of development. 32X.

Fig. 1d - Enlarged version of the same showing different sized follicles. 100X. G - Granulosa.

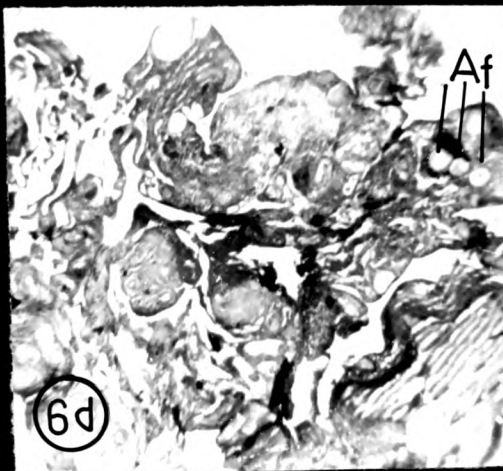
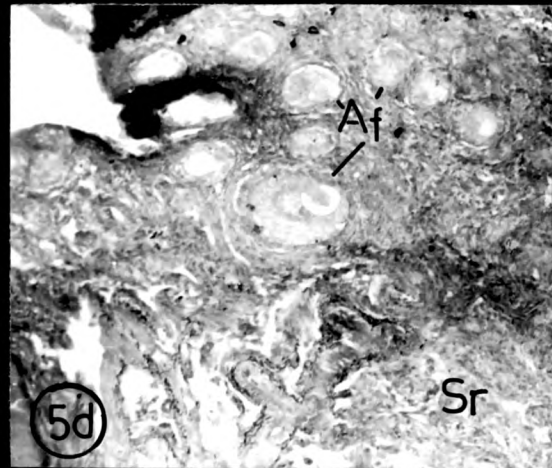
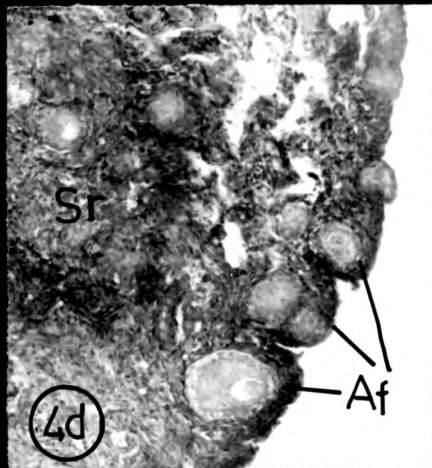
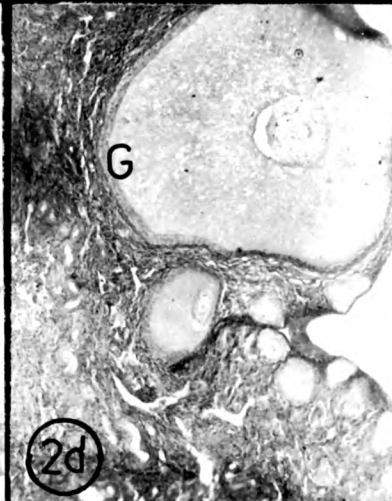
Fig. 3d - Ovary of birds treated with 120 μ g dxm during recrudescence. 32X.

Figs. 4d

& 5d - Enlarged version of the same showing increased stromal basophilia(S~~x~~) and smaller follicles with degenerative changes (Af) 100X.

Figs. 6d

& 7d - Ovary of birds treated with 160 μ g dxm during recrudescence. 100X. Note the extensive stromal disruption (Sr) and highly atretic follicles (Af).

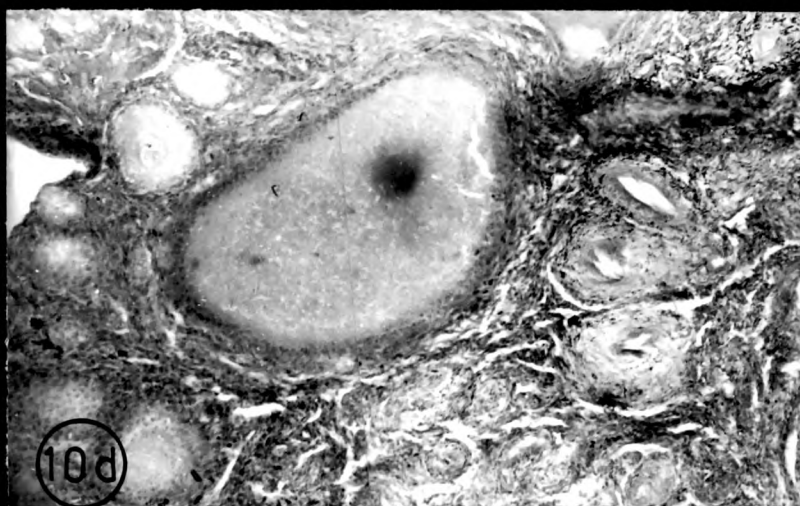
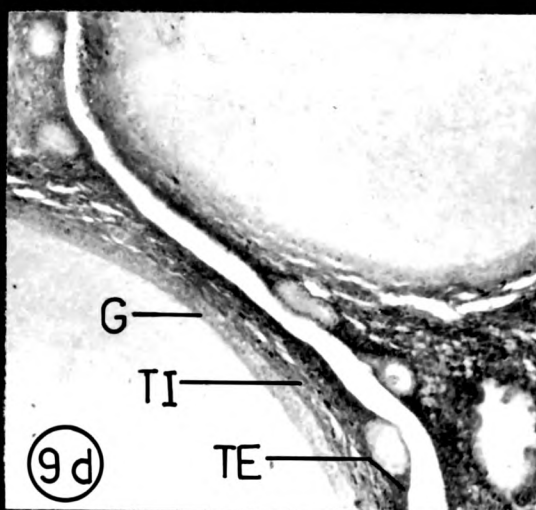
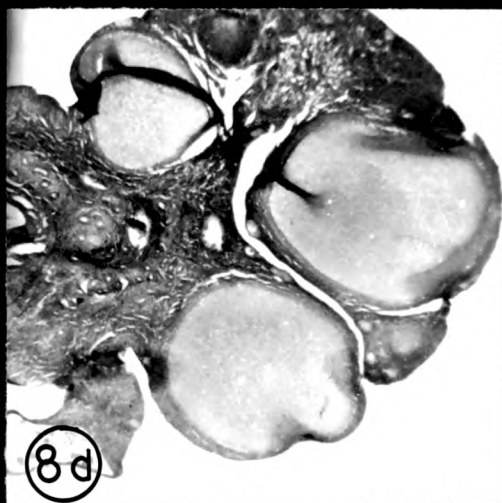


EXPLANATION TO FIGURES.

Fig. 8d - Photomicrograph of the ovary of normal pigeon during breeding showing bigger follicles. 32X.

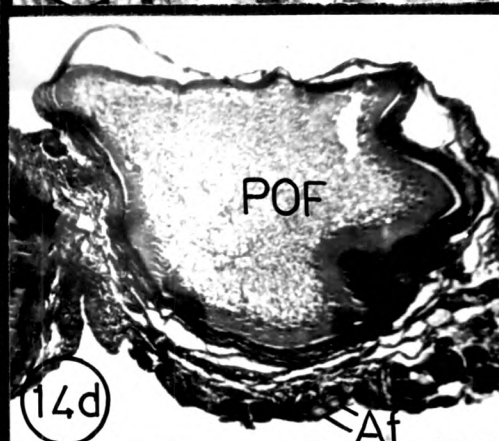
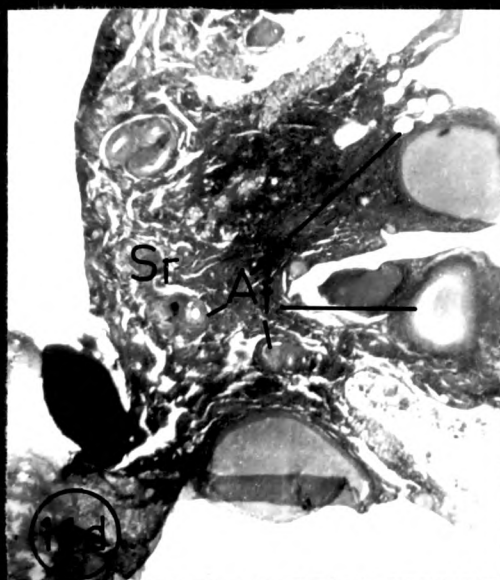
Fig. 9d - Enlarged version of two adjacent follicles showing granulosa (G) and theca interna (TI) and theca externa (TE). 200X.

Fig. 10d - Ovary ^{of} normal birds during breeding showing active follicles. 100X.



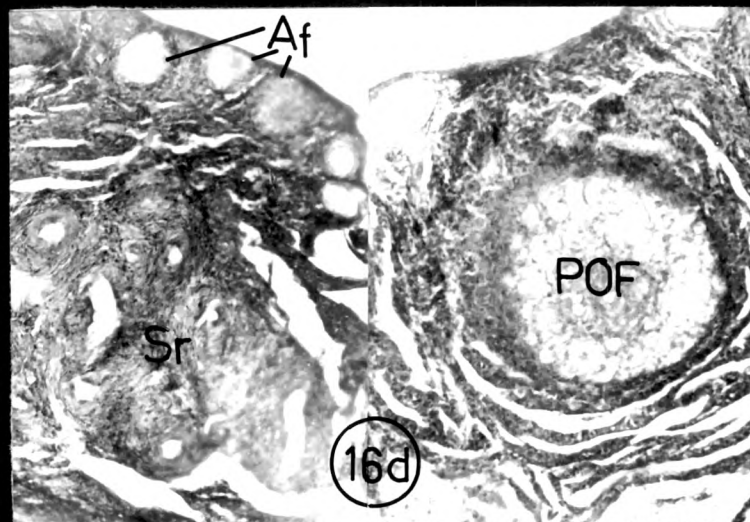
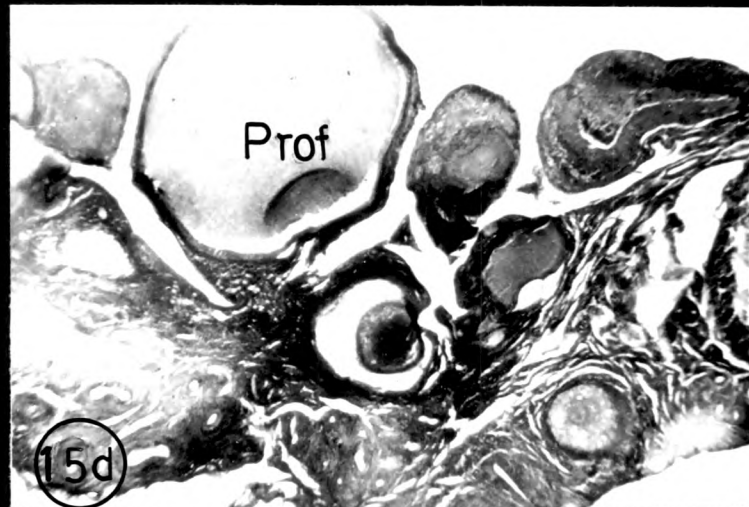
EXPLANATION TO FIGURES

- Fig. 11d - Photomicrograph of the ovary of pigeons treated with 80 μ g dxm during breeding showing stromal (Sr) lesions and atretic (Af) follicles. 32X.
- Fig. 12d - Enlarged version of the same showing marked follicular atresia (Af). 100X.
- Fig. 13d - Further enlargement of the same 200X (Af - Atretic follicle)
- Fig. 14d - Ovary of pigeon treated with 120 μ g dxm during breeding showing atretic follicles (Af) stromal contraction, and degenerating pre-ovulatory follicle (POF) 100X.



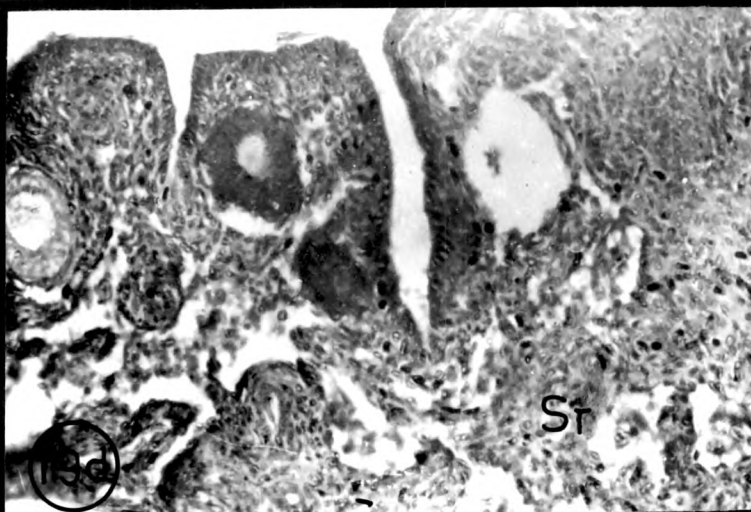
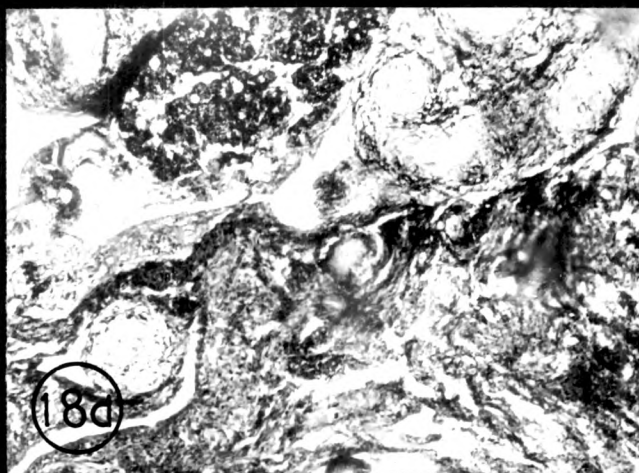
EXPLANATION TO FIGURES

- Fig. 15d - Photomicrograph of the ovary of pigeon treated with 160 μ g dxm during breeding showing extensive stromal disruption (Sr) and atresia of follicles (Af) at various stages of development 32X. POF - Post-ovulatory follicle.
- Fig. 16d - Ovary of pigeons treated with 160 μ g dxm during breeding. 100X. POF - Post-ovulatory follicle, Sr - stroma Af - Atretic follicles.



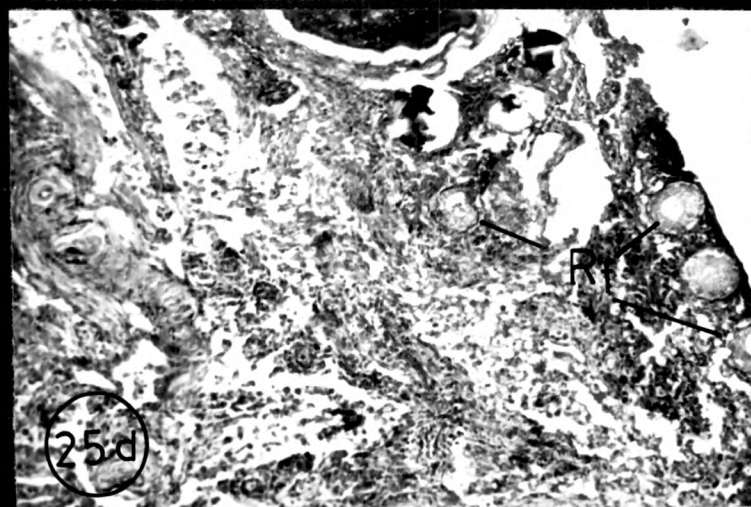
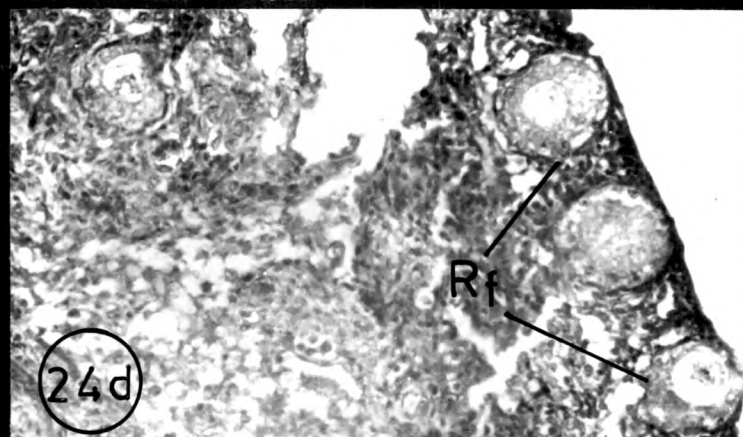
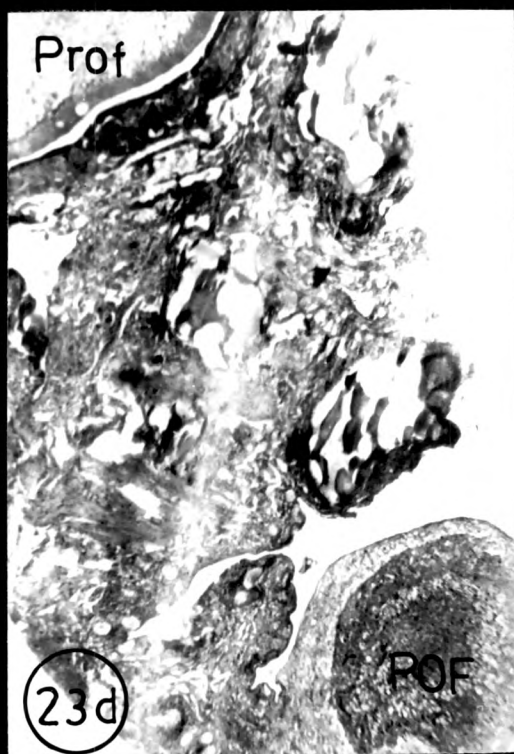
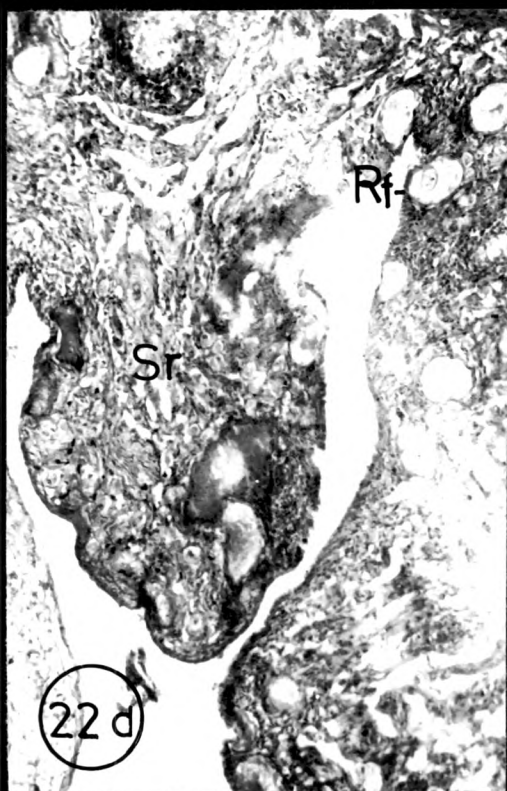
EXPLANATION TO FIGURES


- Fig. 17d - Photomicrograph of ovary of normal birds during regression. 32X.
- Fig. 18d - Enlarged version of the same. 100X
- Fig. 19d - Ovary of pigeons treated with ACTH during regression. 200X. Note the increased stromal (Sr) compactness.
- Figs. 20d - Ovary of pigeons treated with low corticos-
& 21d terone morning dose during regression. 100X. Note the increased stromal compactness (Sr) and follicular recovery (Rf).



EXPLANATION TO FIGURES

- Fig. 22d - Photomicrograph of the ovary treated with low corticosterone evening dose during regression 100X. Stromal compactness (Sr) and follicular recovery (Rf) are evident.
- Fig. 23d - Ovary treated with low corticosterone evening dose during regression. 200X.
POF - Post-ovulatory follicle
PrOF - Pre-Ovulatory follicle
- Fig. 24d - Ovary treated with high corticosterone morning dose showing stromal compactness (Sr) and follicular recovery (Rf). 200X.
- Fig. 25d - A lower magnification of the same 100X.



characterised by peripheral vacuolisation and disruptive changes in granulosa and thecal cells. Hypertrophy of granulosa cells with nuclear pycnosis were clearly evident (figs. 3d to 5d). 160 μ g dxm treatment exhibited more degenerative changes affecting both stromal tissue and follicles. Many follicles showed intrafollicular degeneration and increased basophilia of the stromal tissue. Atretic primary follicles were also evident with accumulation of cell debris in the centre. Large pre-ovulatory follicles also depicted degeneration. Changes affecting granulosa and thecal layers were very much pronounced and gave a disrupted appearance. The granulosa cells were hypertrophied with pycnotic nuclei (figs. 6d and 7d). Dxm treatment during the breeding phase resulted in generalised loosening of stromal tissue with marked disruptive changes. 80 μ g treatment induced atretic changes in both theca and granulosa with more prominent degenerative changes affecting the former. Granulosa cell nuclei depicted pycnotic changes (figs. 11d to 13d). More or less similar changes were shown with 120 μ g treatment as well (fig. 14d). 160 μ g treatment depicted apart from the above mentioned changes complete regression of granulosa (figs. 15d and 16d). ACTH administration induced  prominent rejuvenating changes in the stromal tissue. Though most of the follicles still appeared atretic with no signs of

follicular development, the general appearance tended to indicate a check on the regressive changes characteristic of non-breeding phase (fig. 19d). Corticosterone treatment (LCM) brought about increased compactness of stromal tissue and a noticeable activation of the follicles marked by the regeneration of granulosa and a less defined theca (figs. 20d and 21d). LCE and HCE showed some reparative changes in the form of stromal compactness and revival of ^{the} granulosa (figs. 22d and 23d). However HCM appeared to show more marked regenerative changes in the ovary (figs. 24d and 25d).

DISCUSSION

Seasonal breeders like aves regulate their breeding activities by a cascade of actions involving environmental cues, central nervous mechanisms, neuroendocrine transducers and the hypothalamo-hypophysial system leading to the release gonadotrophic hormones which ultimately induce steroidogenesis and gametogenesis in the gonads. This central axis which regulates annual gonadal functions in seasonal breeders is however not an independant invariable axis as many physiological and endocrine factors are capable of interacting at different levels so as to regulate the breeding activities of a species. Two of the endocrine glands that have been known to undergo seasonal alterations

in relation to annual gonadal cycle in aves are, the adrenal and ^{the} thyroid. Though the sites and mode of actions of the secretions of these glands with reference to the central axis are not clear, both parallel (progonadal) as well as inverse (antigonadal) relationship with the gonads have been demonstrated (Thapliyal and Pandha, 1967; Thapliyal et al., 1968; Jean et al., 1977; Aznar et al., 1978; Chaturvedi and Thapliyal, 1980; Johnson et al., 1982; Wilson, ^{and Louis,} 1982; David et al., 1982; Suresh and Chaturvedi, 1984).

The present histological study on wild pigeons has demonstrated a parallel adrenal-gonad axis and an inverse thyroid-gonad axis as has been inferred previously by the seasonal changes in weights of these organs. This becomes evident by the observed adrenocortical activation and reduced thyroid functioning during the recrudescence and breeding months whence both the testis and ovary were found to be functionally active. Changes marked by adrenocortical regression and increased thyroid activity in the non-breeding phase illustrate this aspect further. Apparently an inverse relationship between the adrenal and thyroid can be presumed which may have a significant bearing from the point of view of the many physiological and metabolic changes that have been noted to occur in relation to gonadal cyclicity (Chapters, IV, V, VII, VIII).

The existence of a parallel adrenal-gonad axis that was inferred from the observations made during ^{the} three reproductive phases in normal birds was further confirmed by the observed shrinkage of the gonads accompanied by degenerative changes affecting both the testis and ovary brought about by the experimental suppression of adrenocortical activity by dxm during the reproductively active phases. Suppressive effect of dxm on adrenal function has been demonstrated in a number of species including man (Justiniano et al., 1979; Jones et al., 1979; David et al., 1980; Bhattacharyya et al., 1980; Britton et al., 1986). Both surgical as well as chemical adrenalectomy (by dxm) have been reported to induce marked atretic changes in the ovary as well as degenerative changes affecting seminiferous tubules and interstitium of the testis in immature and mature rats (Wolf and Leathem, 1955; Choudhary and Chatterjee, 1978; Tanaka and Yasuda, 1980; Kruger et al., 1982). Though the actual mode of action of the adrenal gland is not yet clearly outlined, Alterman (1956) had reported reduced gonadotrophic concentration after adrenalectomy in mature rats. Moreover, Pandey et al. (1978) have shown the favourable role of adrenal steroids in ovulation in the gold fish in relation to the temperature of the medium.

Subsequent to the observation of gonadal regression due to adrenocortical suppression by dxm in the recrudescence

and breeding phases, the possible ability of ACTH or corticosterone to induce gonadal activation during the regression phase was evaluated. Treatment with ACTH (0.5 I.U./bird) or LCM (1 µg/bird) given for 10 days induced noticeable changes in both testis and ovary suggestive of activation. The activation changes were more pronounced for testis than for ovary. Although the basal germ cell layers (spermatogonia and spermatocytes) seemed to have regenerated considerably, no spermatids were however visible. On a comparative basis, corticosterone administration depicted more progressive regeneration changes of the germinal epithelium than ^{with} ACTH administration. Apparently, ACTH induced changes are also essentially mediated by bringing about release of corticosterone from the adrenals. Though the ACTH and LCM induced changes were more markedly pronounced in the testis than in the ovary, HCM induced more regenerative changes in the ovary, as was earlier inferred based on the observed changes in gonadal weight. This may suggest an apparent sexual dimorphism in circulating levels of corticosterone. Neither the evening schedule nor the high doses of corticosterone were able to induce changes as prominent as LCM with regard to testis. Apparently diurnal mechanisms can be considered to be operative in the pigeon which was well exemplified by the changes in many biochemical parameters noted in the present study with the different corticosterone dose regimes.

A literature scan indicates a number of reports suggesting an inhibitory action of ACTH in sexual functions. Many of these studies carried out in immature and virgin female mice or infantile female rats have shown effects ranging from delayed onset of estrous and decreased ovarian weight and suppression of vaginal estrous with reduced weights of ovary, vagina and uterus (Jarret, 1965) to inhibition of sexual maturation (Christian, 1964) and inhibition of PMS induced ovulation ^{Hagino et al.} (1969). Flickenger (1966) has also shown disruption of ovulation with high doses of corticosterone in *the* domestic hen. Moreover, Chaturvedi and Thapliyal (1980) have also demonstrated corticosterone induced gonadal inhibition in the common myna. In contrast to these are the reports indicating the ability of exogenously administered ACTH to maintain spermatogenesis in mature hypophysectomized rats (Li and Evans, 1947; Chatterjee, 1967; Goldman and Yakovac, 1968). Another report of significance is that of Sunderraj and Goswami (1966) who in their studies have seen the attenuating influence of pretreatment of metapirone on the ovulatory capacity of LH in hypophysectomised gravid females ^{of *H. Fossilis*.} Further ^{both} they demonstrated that ^{both} deoxycorticosterone acetate and hydrocortisone acetate, induced ovulation and/or spawning regardless of pretreatment with metapirone. These reports clearly underscore the possible species differences as well as the ability of corticosteroids to act at different

levels of the central axis and/or even on the gonads directly in modulating the structural and functional^{aspects} of gonads. The present study has revealed the possible direct and indirect influence of corticosteroids in controlling seasonal gonadal activities in birds. The inability of the present study to bring about complete spermatogenesis and folliculogenesis may be attributed to the short duration (10 days) of treatment which obviously is insufficient for complete activation of the gonads from a regressed condition. Besides, the balanced interplay of both adrenal and thyroid secretions in optimising the gonadal responses cannot also be overlooked as changes of definite nature have been noted to affect the thyroid during normal seasonal cyclicity as well as under experimental manipulation of the adrenals.

S U M M A R Y

Histological changes in gonads, adrenals and thyroid have been studied during different phases of breeding as well as under conditions of adrenal manipulation in Columba livia. Increased adreno-cortical activity along with active functional gonads and reduced thyroid activity were observable during the recrudescence and breeding seasons. The non-breeding phase was marked by a reverse set of changes with increased thyroid activity coupled with reduced adreno-cortical activity and regressed gonads. These changes were mimicked by dexamethasone induced adrenal suppression in the breeding phases. Similarly, ACTH/corticosterone treatment in the non-breeding phase induced changes which were comparable with those occurring during a normal recrudescence phase. The results portray a parallel adrenal-gonad axis and inverse adrenal thyroid axis in tropical Indian pigeons.