CHAPTER : 2

SOME OBSERVATIONS ON THE ANNUAL OVARIAN CYCLE – A
HISTOMORPHOLOGICAL AND FIELD STUDY

Many of the species of crows (Family : Corvidae) are
so nearly similar in gross outward appearance that they are
almost impossible to identify with certainty in the field
on the basis of morphology and colour alone. In such a
confusing group, it is important to have a comparative
information on the biology of the individual species. Such
information on breeding biology combined with morphologic
characters can be of primary importance in working out
the relationships of the species involved. Some
biological information is available for certain species
(Ali, 1926; Lamba, 1963; 1965a, b; 1969), others are
poorly known. The Rook (Corvus frugilegus), which to
date, is the only seasonally breeding wild species
that has been studied in detail for its ovarian cytology
Avian studies reveal a consideration interspecific diver­
sity in the length of the breeding season and response
to photoperiodic variation (Lofts and Murton, 1968).
Unlike the situation in male, the functional morphology
of the female gonad has been studied very little in wild
species. Literature on cyclic changes of the avian ovary is sparse and very little is known beyond the follicular activity of the domestic species. Data on the histophysiological changes on the ovary of seasonally breeding birds throughout the year are almost non-existent or have been reported rarely. Much of the information has been derived almost exclusively from investigations on the domestic fowl. Literature on ovarian cycles in birds has been reviewed by Brambell (1956) and Mathews and Marshall (1956).

The Indian house crow is a prominent species in many parts of India. However, with the exception of a report by Lamba (1963) and few others (for references see Chapter I) regarding breeding biology and determinate laying pattern, not much information is available on the ovarian cycles of Indian house crow. Previous studies, (Lehrman, 1961; Marshall, 1961; Van Tienhoven, 1961; Farner and Follett, 1966) concerning behavioural and ecological factors influencing reproduction in birds have amply emphasized the value of field investigations in studying reproductive processes and have suggested a need for further work which would correlate environmental, behavioural and physiological events. The present study therefore, was carried out with
concurrent attention to behavioural and histological ovarian changes in an attempt to determine ovarian correlates of reproductive physiology in Indian house crow population from a restricted area – Baroda – situated along the Western Coast of India.

Ovarian histology is accorded special attention in this study because characteristics of seasonal ovarian changes and factors influencing these changes in general are poorly understood (Mistra, 1960–61; Marshall, 1961; Lamba, 1963; Farmer, 1964; Farmer and Follett, 1966). Yolk-formation has been studied only in the starling, Sturms vulgaris (Bullogh, 1962), the Rook, Corvus frugilegus (Marshall and Coombs, 1957) and Blackbilled Magpie, Pica pica (Erpino, 1969). Considering the above mentioned lack of sufficient information, particular attention has been directed to gross morphological and histological variations in ovary of adult female crows throughout the year. Additionally, an attempt was made to present graphically, in an integrated form, the possible relation of the observed facts on the sequence and timing of behavioural, physiological and morphological events in adult crows. Furthermore, testicular (Chapter 1) and oviducal weight cycles of this bird have been taken into consideration for the interpretation.
of the ovarian cycles (Figs. 2 and 3) for discussion purposes. Such an approach may prove to be useful in deciding whether the house crows breed once or twice in an year and when.

MATERIAL AND METHODS

During a four and a half year period (from January, 1971 to June, 1975), a total of 307 Indian house crows, Corvus splendens, were captured from the study area (Baroda - India). Most of the birds were shot dead on the University Campus, while a few were dissected in the laboratory itself and ovaries were removed within minutes from the birds and fixed in Bouin's fluid. They were weighed accurately. Diameter (to the nearest 0.1 mm) of the largest ovarian follicle, was recorded in non-laying females and diameters of the larger graded follicles (see Van Tienhoven, 1961) were noted in laying birds. Oviducts were excised and fixed for three days in Bouin's fixative and were weighed on metler balance. All tissues were embedded in paraffin wax. Follicles larger than 5 mm in diameter were removed before embedding and measurements from these are not included in table: 3. 6 μ thick sections of both the tissues were cut and stained with
Ehrlich's haematoxylin-eosin and Masson's trichrome techniques. Qualitative features of the ovarian stroma, stromal glands, healthy follicles and their thecae, post-ovulatory follicles and atretic follicles were noted. Mitotic frequency in the granulosa of healthy follicles was noted. Atretic follicles were distinguished from older postovulatory follicles according to criteria adopted by Erpino (1969). In general postovulatory follicles were irregular or angular, flat or collapsed structures. In such follicles granulosa cells remained in close association with basement membrane in early stages; necrosis occurred when cells slough off. Yolk was not seen within the lumen, and lack of vascularity and phagocytic invasion were characteristic features of post-ovulatory follicles. In early stages ruptured thecal layers were folded in, and merging imperceptibly with ovarian stroma in older samples. While atretic follicles were round, (having separated granulosa cells which moved away from basement membrane in early stages) cellular hypertrophy was a common feature. In many follicles yolk was often present; thecal vascularity remained persistent through rupture of thecal layers was not apparent in all non-bursting (yolky) atretic follicles. At least five different representative sections in each case were examined for counting healthy atretic follicles. Relative estimates of size (diameter)
were made by recording the number of intersects occupied by the follicular diameter on an ocular micrometer. Primary follicles were not included in these counts. The gonosomal index (GSI) was calculated for every month as below:

\[
\text{GSI} = \frac{\text{Weight of ovary}}{\text{Weight of bird}} \times 100.
\]

PERIOD OF LAYING:

The period of laying was determined by examination of the ovaries of laying females. A bird was considered to have started laying if the follicles were large and at least one large postovulatory follicle was present. Laying was considered to have terminated if the preovulatory follicles were small and numerous postovulatory follicles were present. The duration of laying, derived by this means and field observations of nests has been represented by a horizontal bar. Major physiologic and behavioural features were noted by carrying out field-studies and every year at least 3 nests were examined and whenever it was possible, birds were killed in the field to correlate ovarian cycle with these features.
OBSERVATIONS

FIELDS OBSERVATIONS ON BREEDING BIOLOGY OF FEMALE CROW (Corvus splendens):

In the previous chapter, which deals with the testicular cycle of this bird, the same cycle has been divided into preparatory, progressive, breeding and regressive phases for description and discussion purposes. Here, growth phases during ovarian cycle have been found to fall into following seven categories according to social structure, physiological state and behavioural changes related to the reproductive cycle:

(1) WINTER (PRE-BREEDING): Represents pre-breeding phase or preparatory period of the ovarian cycle which begins from November and lasts until the 2nd week of April.

(2) PURSUITS AND PARTIS: The period was normally characterized by such behavioural patterns as chasing, fighting and chiefly by establishment of pairs. Once a pair bond was established it was maintained approximately three to three and a half months period. Pairs get established by the third week of April and last until the first week of August.

(3) NEST-BUILDING: In the month of May mating as well as nest-building activity continued until first week
Fig. 1: Annual changes in (a) social behavior* in Corvus splendens, with associated changes in (b) mean diameter of largest ovarian follicle.


Fig. 2: Annual variations in ovarian and oviducal weights. Each dot represents individual ovarian weight.
**Fig. 3:** Integration of trends in some major physiological features (ordinate) with that portion of the annual cycle investigated (abscissa). The distance between perpendicular lines on abscissae indicates relative length of time (see text for detail) involved in each stage of the cycle by a pair of Indian house crows. Curves for each physiologic category were derived by designating time of maximum development or activity as 100% and then plotting seasonal variations thereof. $P. - O.F.$ indicates post-ovulatory follicles.

<table>
<thead>
<tr>
<th>Stage</th>
<th>WINTER</th>
<th>PERSUITS</th>
<th>CORTISOL</th>
<th>LAYING</th>
<th>HATCHING</th>
<th>POST HATCHING</th>
</tr>
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<tbody>
<tr>
<td><strong>A. Male system:</strong></td>
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<tr>
<td>Testes weight</td>
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<td>Spermatogonia</td>
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<tr>
<td>Diameter of epididymis</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Spermatozoa diameter</td>
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<td><strong>B. Female system:</strong></td>
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<td>Diameter of healthy follicles</td>
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<tr>
<td>Number of P-O.F.</td>
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<tr>
<td>Glandular atretic follicles</td>
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<td>Lipo glandular atretic follicles</td>
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<td>Relay atretic follicles</td>
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<tr>
<td>Stromal glands</td>
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<td></td>
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<tr>
<td>Weight of ovary</td>
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</tbody>
</table>

* Indicates relative percentage occurrence among total atretic follicles found
TABLE 2.1

Showing variations in gonosomatic index and size of follicles

<table>
<thead>
<tr>
<th>Months</th>
<th>Total No. of birds</th>
<th>Mean body weight (GM)</th>
<th>Mean absolute ovarian weight (GM)</th>
<th>GSI</th>
<th>No. of birds with follicles in size group</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Under 3 mm</td>
</tr>
<tr>
<td>January</td>
<td>25</td>
<td>254</td>
<td>0.1033</td>
<td>0.4061</td>
<td>23</td>
</tr>
<tr>
<td>February</td>
<td>28</td>
<td>260</td>
<td>0.1264</td>
<td>0.4862</td>
<td>10</td>
</tr>
<tr>
<td>March</td>
<td>31</td>
<td>270</td>
<td>0.1805</td>
<td>0.6685</td>
<td>3</td>
</tr>
<tr>
<td>April</td>
<td>32</td>
<td>278</td>
<td>0.3326</td>
<td>1.1964</td>
<td>2</td>
</tr>
<tr>
<td>May</td>
<td>17</td>
<td>248</td>
<td>0.7428</td>
<td>2.9952</td>
<td>0</td>
</tr>
<tr>
<td>June</td>
<td>23</td>
<td>337</td>
<td>5.8968</td>
<td>17.2012</td>
<td>0</td>
</tr>
<tr>
<td>July</td>
<td>25</td>
<td>277</td>
<td>2.3259</td>
<td>8.3968</td>
<td>0</td>
</tr>
<tr>
<td>August</td>
<td>25</td>
<td>288</td>
<td>0.1429</td>
<td>0.3962</td>
<td>6</td>
</tr>
<tr>
<td>September</td>
<td>25</td>
<td>222</td>
<td>0.0664</td>
<td>0.2991</td>
<td>23</td>
</tr>
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<td>October</td>
<td>24</td>
<td>253</td>
<td>0.0440</td>
<td>0.1739</td>
<td>22</td>
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<tr>
<td>November</td>
<td>24</td>
<td>292</td>
<td>0.0622</td>
<td>0.2130</td>
<td>21</td>
</tr>
<tr>
<td>December</td>
<td>27</td>
<td>291</td>
<td>0.0864</td>
<td>0.2969</td>
<td>24</td>
</tr>
</tbody>
</table>
Characteristics of healthy and atretic follicles (AF) in ovarian sections from Indian house crow (Corvus splendens) collected during 1971-1975.

<table>
<thead>
<tr>
<th>Stage in Cycle</th>
<th>Healthy Follicle</th>
<th>Atretic Follicle</th>
</tr>
</thead>
<tbody>
<tr>
<td>POST-BREEDING</td>
<td>196.8 ± 22.76</td>
<td>N/A</td>
</tr>
<tr>
<td>INCUBATION</td>
<td>368.6 ± 94.65</td>
<td>N/A</td>
</tr>
<tr>
<td>LAYING</td>
<td>173.4 ± 22.18</td>
<td>N/A</td>
</tr>
<tr>
<td>POST-BREEDING</td>
<td>226.6 ± 60.78</td>
<td>N/A</td>
</tr>
<tr>
<td>POST-LAYING</td>
<td>180.0 ± 33.26</td>
<td>N/A</td>
</tr>
<tr>
<td>POST-LAYING</td>
<td>N/A</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Note: 'n' represents the total number of observations. SD computed from mean values among birds from a particular collection period.
of June. Nests were built once in a year and they were never utilized second time. Crows and even other birds do not remove the nest once constructed but it gets spoiled by natural forces like rain and wind. The observations cited herein are based on the study carried out at three different sites: (i) the area in and around the M.S. University campus - Baroda, (ii) Gujarat State Fertilizers Factory and Colony area, Northen Baroda, seven kilometers away from University Campus area, (iii) State Reserve Police Training Ground - Southern Baroda, five kilometers away from University Campus area. Nests were built-up on trees like Black plum tree (Java apple or Jambu tree) Eugenia jambolana Lam., Blue gum tree (Eucalyptus tree), Eucalyptus globulus, and the Royal gulmohar tree (Flamboyant tree), Delonix regia. Generally it was observed to have 1:1 or 2:1 ratio for nest number to tree number. It was an interesting observation that every year the crows preferred the above mentioned sites repeatedly to construct nests and in each area under observation nearly fifteen nests were easily noticed every year. All the sites were very much close to human residential colonies or University Students Hostels. The birds make a thick platform of the dry sticks with a central depression (cup lined with thin soft sticks or grass material) for egg-laying; generally at about
25-30 ft. or above the ground level. Crows have been seen to construct nests rarely in the last week of April; but by the 1st week of May, nest building activities were very common and in most of the cases by the 1st week of June, nests were completed. Generally, a pair takes totally 10 to 11 days to complete a nest. Lamba (1963) has reported a shorter period of total 4 to 7 days. The total period (33 days) of nest building for small populations under investigation has been divided into the following three stages with reference to accompanying ovarian histological changes:

(a) Early stage: 1st of May to 17th May. Sticks are arranged in a fork of three branches in a criss-cross manner forming a circular platform.

(b) Mid stage: 18th May to 26th May. After 3 to 4 layers of sticks laid in the platform, additional sticks were observed to be arranged tangentially so that a shallow cup-like structure (7-10 cms high and 5 to 9 cms wide) was formed.

(c) Last or Completion stage: 27th May to 3rd June. Instead of dry thick sticks, now the crows used green and wet grass, grass roots and vegetable material to line the nest. Sometimes soft feathers were also used for flexibility. Now the nest measured 7 to 10 cms in depth, the outer diameter was about 25-31 cms and the inner diameter about 12-16 cms. It was impossible to identify the sex from distance and due to this reason, it was difficult to judge about partici-
pation by male crows in nest-building activity; nevertheless, it was easy to observe that, from a pair, both the individuals brought suitable nest-material.

(4) EGG-LAYING (1st June to 10th July): Four or five eggs were laid normally at intervals of 1-2 days in the month of June or sometimes in 1st and 2nd week of July. In majority of the cases after the first showers of rain i.e. around 15th of June, most birds had laid the eggs.

(5) INCUBATION (15th June to 28th July): The incubation of eggs was not done exclusively by the female bird but the male often took part in incubation of the eggs with the parent birds relaying each other at an interval of approximately two hours. The incubation period was 15-17 (average 16, n = 6) days. (Lamba, 1963 reported this period to be of 16 to 17 days duration).

(6) NESTLING (24th June to 12th August): The duration of time between laying of the last egg and the appearance of the last hatchling was about 27 to 30 days. The young ones hatch out one after the other at intervals of 1-2 days. Nestlings left the nest approximately after 4 weeks. The newly hatched nestling was feathered with gray-black down. Its eyes were closed. The nestling opened the eyes after 2-4 days (n=12), when it could
insert its beak into the beak of parents for getting food. Both the sexes took part in feeding the young ones.

(7) POST-BREEDING REGRESSION (15th August to 30th October): Pair-bonds were observed to break during this period, usually in the month of August only. No overt behavioural characteristic features in regard to social interaction related to reproduction were observable in this phase.

OVARIAN WEIGHT VARIATION CYCLE:

Seasonal trends in ovarian weight changes of the Indian house crow (Corvus splendens) are presented in Fig. 2 and table 2.1. It could be seen that the ovaries of adult females began to increase in weight and size by mid-November. A gradual increase was maintained throughout winter, reaching mean wintering weight of 0.1805 gm in February. By about mid-April ovaries depicted a rapid growth phase and the ovarian weight reached a maximum mean weight of 5.7968 gms in June. (Birds (n=4) of nest-building period averaged 1.088 gms of ovarian weights). The weight of ovaries of actively laying birds, varied from 5.500 to 8.100 gms (mean = 6.770 gms during June and July, n = 10). An increase to the tune of 681.55% during the transitory period from May (nest-building
period) to June (laying period) suggested an abrupt change. In late July a lower mean weight of 2.325 gms was recorded though the early part of this month was considered as the laying period, suggesting that the decline in weight was primarily due to completion of laying. Unlike the gradual and slow increase in the weight during the 5 months period (mid-November to mid-April), the fall in weight during post-laying period (July and August) was very abrupt. It took hardly fifteen days for ovarian regression to occur which was evident from the weight change between July and August; accounting for 93.65% decrease in mean weight. When considered in terms of gonosomatic index (GSI) (Table 2.1) showed parallel trends in general with absolute ovarian weight cycle. The highest GSI (average = 12.7990) was recorded for breeding phase and lowest (average = 0.3231) for regression phase. The patterns of GSI variations coincided well with the histological data which pertain to the mean diameter values of the large ovarian follicles, and in case of males with the testicular and epididymal cycles (Figs. 1b and 3).

MICROANATOMY:

Essentially, the ovary consisted of medulla and cortex separated by a dense layer of connective tissue,
the tunica albuginea. The medulla contained connective tissue, nerves and smooth muscles. It was the most vascular part of the ovary. The cortex contained the primary ovarian follicles and surrounded the medulla completely except for the hilus. Its outer surface was covered by cuboidal epithelium which became flattened as follicles grew and bulged out from the surface.

ANATOMY OF THE MATURE FOLLICLE:

The wall of the mature follicle consisted of the following characteristic regions (Fig. 1, 18, 19 and 20): (1) membrana granulosa (2) theca interna and (3) the theca externa. The zona radiata, was a narrow zone (5 μm wide) present in all follicles over 6 mm diameter (Figs.18, 19 and 20). Zona radiata was the region of contact between oocyte and follicle. Membrana granulosa was found to grow in thickness as the oocyte grew by proliferation of granulosa cells. Initially, in immature (growing) follicles, the cells (more or less columnar or cuboidal) were arranged in a layer of single cell thickness (Fig.9), which later on assumed multilayer character, having three to four cells (stretched and flattened) thickness in fully mature follicles. The theca interna was a compact cellular capsule containing a narrow inner layer of collagen fibres, a middle layer
of fibroblasts and an outer layer of vacuolated cells. Theca extern was wider and looser than the theca interna and consisted of rows of fibroblasts interspersed with collagen fibres. The follicle was covered by a loose connective tissue containing smooth muscle and this connective tissue was negligible over the stigma.

The immature follicle (30.0 to 50 μ) remain, generally embedded in cortex and received blood from small arterioles. The mature follicle had an extensive vascular system. The stigma was a specialized region of the follicle where at ovulation a split occurred to liberate the oocyte. Macroscopically it was a pale band about 1.5 or 2.5 cm long running across the apex of the follicle (Fig. 5) and was supplied with but a few small veins and arteries. Structurally it was similar to, but thinner than, the follicular wall in other regions; stroma of the ovary contained stromal glands and different types of atretic follicles but a 'scar' was never found in any section of ovary observed during this study.

ANNUAL CYCLE OF OVARIAN FOLLICLES (Healthy Follicles):

Largest ovarian follicles and postovulatory follicles: Distinct follicles were not discernible in the ovaries during morphologic studies on the ovaries of young
juvenile females captured in August and September. While during November and December, the ovary appeared to possess only indistinct protuberances less than a tenth of a millimeter in size. In the month of February almost all samples collected showed distinct follicles of smaller size. It was observed that though the ovary was increasing in weight and size, from end of October as indicated in fig. 2 and table 2.1, the follicles remained in a rudimentary condition until mid-December, when they began to enlarge in preparation for the ensuing breeding season. The largest follicles in October averaged 0.98 mm in diameter. In late November the follicles began to enlarge gradually, the rate of growth was very slow, like the rate of increase in weight.

From 1.2 mm (mean diameter of largest follicles) to reach 3.0 mm size, it took four months. During late February and March, the growth rate was slightly higher; as in March it reached 5.5 mm (mean diameter of largest follicles) size as against 3 mm in early February. The growth rate was maintained at a higher level upto May. By the second week of May adult birds had ovarian follicles approaching the ovulatory size of 12.9 mm. Follicles of ovulatory size (Fig. 5) could be encountered until the end of the 1st week of July. No females with large un-
ovulated follicles were found later than July 12th. The unovulated or atretic follicles were rapidly resorbed. By the last week of July or first week of August the overwintering follicular size of 0.98 mm was reached. Diameter of largest ovarian follicles averaged 2.22 mm in winter and about 12.90 mm just prior to breeding season (last week of May). In early nest-building period it measured 11.08 mm and reached 13.66 mm size, during the completion of nest building period. Largest ovarian follicles in the egg-laying period were 14.9 to 15.8 mm in diameter. This represented the ovulable follicular size for this bird (*Corvus splendens*). A few out of many larger follicles showed further enlargement after the nest-completion period while a reduction in number of large follicles was noted in females nearing completion of the clutch (i.e. entering the post-ovulatory period or incubation period). Neither bursting atresia (Davis, 1942b) of larger follicles at the time of cessation of laying (in mid and late July) nor flaccid atresia (Berry, 1962) of mature follicles was observed in Indian house crows. Post-ovulatory follicles (Figs. 6, 7, 8) regressed rapidly after ovulation. Approximately two days after ovulation had occurred, the granulosa layer thickened but the integrity of cells was maintained and were abutting to the basement membrane. Blood cells appeared in lumina of
recently ovulated follicles (Fig. 17); thecal layers, thickened a bit and some proliferation of presumed thecal gland cells persisted during this period. Beginning about 4 days after ovulation, granulosa cells, with some phagocytes too, began sloughing off into the follicular lumen. Shortly after the dissociation of granulosa layer had occurred, the sloughed cells became vacuolated and possessed pycnotic nuclei. Subsequent degeneration was rapid and as early as day ten of incubation the follicular traces were not discernible. Older post ovulatory follicles could no longer be distinguished with certainty from larger, degenerating yolky atretic follicles. Post ovulatory follicular apparatus resembled in many ways the varying stages of lipoglandular atretic follicles. Occurrence of phagocytosis of granulosa cells, necrosis of thecal cells and absence of thecal vascularity indicated that post ovulatory follicles were shortlived. Measurements of the largest ovarian follicles in last week of June to first and second week of July (incubation period) and first week of July to last week of August (nesting period) revealed pronounced follicular regression (Table 2.2; and Figs. 1b, 3). In three (n = 3) incubating birds the largest ovarian follicle averaged 4.91 mm, while in four (n = 4) birds with nestlings, the largest follicles averaged 3.60 mm in diameter.
Results of histologic measurements of healthy follicles are presented in table 2.2. In particular, the reduction in size of such follicles was very much in evidence, late in the laying period and nestling period as opposed to the early laying and incubation periods.

In all collection periods, larger healthy follicles had stratified granulosa. Small young follicles (59.94 to 106.56 μ in diameter) were covered by granulosa having single cell thickness. Gradual increase in follicular diameter did not register a proportional and simultaneous increase in the height of granulosa layer and such follicles (having diameter of 2.46 mm or less than this) had one cell thick granulosa layer. Multilayered granulosa was evident only in follicles measuring more than 2.5 mm in diameter. The height of granulosa layer measured 9.99 μ to 11.66 μ in follicles (n=18) having one cell thickness, 16.65 μ to 19.98 μ in two cell thick granulosa (n=10), and 26.64 μ to 33.30 μ in three to four cell thick granulosa (n=9) layer. Mitotic activity was noted in the granulosa cells throughout the year cycle, but higher frequency of occurrence was much in evidence during the early and mid-nest building periods (last week of April to the end of May), the egg-laying period (June to mid July) and during incubation (mid July to end of July).
period. Thecal gland cells were present in larger follicles in all collection periods but trends in development could not be understood properly due to following reasons. It was noticed that some birds had small, widely separated thecal gland cells, while other birds captured in the same season, had comparatively larger, more abundant, prominent thecal gland cells. Moreover in the same ovary, thecal gland development varied when comparisons were made between follicles of more or less similar size.

Season-wise analysis also presented less definite growth pattern of thecal gland cells. However, occurrence of only one possible peak in thecal gland cell development was recognizable, which coincided with massive development of stromal glands in females (n=3) captured during the third week of May in mid-nest building stage.

**ATRETIC FOLLICLES:**

Following three types of atretic ovarian follicles (AOF) were distinguished in the Indian house crow (*Corvus splendens*):

1. **Glandular Atretic Follicle (GAF)** (Figs. 13 to 16).
2. **Lipo-Glandular Atretic Follicle (LGAF)** (Figs. 10 to 12).
3. **Yolky Atretic Follicle (YAF)** (Figs. 21 to 28).
GAP: Glandular atretic follicles in various degrees of development are photomicrographically shown in figures 13, 14, 15 and 16. This class of atresia represented initial stages of follicular degeneration. The initial stages of formation of GAP showed a slight dissociation of granulosa cells and often the formation of a narrow band of dense connective tissue immediately peripheral to the granulosa. Further development involved movement of sloughed granulosa cells, usually with large number of phagocytes into the substance of degenerating oocyte. The subgranulosa ring of connective tissue, apparently composed of fibroblasts, maintained separation of granulosa cells and thecal layers. In early stages of dissociation, granulosa cells hypertrophied. Mitotic activity was decreased in the granulosa cells which have begun to slough. In later stages of glandular atresia, granulosa cells often became lipoidal and vacuolated, with shrunken eccentric nuclei. Separation of the granulosa cells from outer thecal layer by connective tissue persisted.

KGAP: Lipo-glandular atretic follicles consisted of a central cluster of lipoidal cells of granulosa origin that was delimited by a thin layer of fibroblasts (Figs. 10, 11, 12). Extending connective tissue septa
enclosed clusters of gland cells of thecal origin. Often, the innermost gland cells were lipoidal. Thecal layers of lipo-glandular atretic follicles were highly vascular. In contrast to glandular atretic follicles, IGAF were rather uniform in size and were noticed less often in most of the ovaries (Table 2.2) and whenever observed were found to be embedded within the ovarian stroma and never on elevated stalks. It was difficult to predict about their (IGAF) origin. However, their round appearance and similarity to enhanced stages of both glandular and yolky atretic follicles, presumably were indicative of their origin, either GAF or YAF.

YAF: It was difficult to trace the 'intermediate' (2-4 mm) YAFs (First type YAF - Erpino, 1969) with ruptured thecal layers (Fig. 24) allowing yolk extrusion. This type of YAF was hardly observed in Indian house ovaries. The other type of YAF (Second type - Erpino, 1969), where yolk extrusion was not apparent and which resembled massive glandular atretic follicles, was very common. The frequency of occurrence of second type of YAF was higher and a number of them were present particularly during the laying and post-laying periods. Here the granulosa cells initially exhibited proliferative activity and later became lipoidal. In some follicles lipoidal granulosa
cells dissociated and moved towards central parts, ultimately disintegrating. In some other follicles, where the granulosa layer showed significantly folded appearance, the constituent cells were seen to remain still attached to the sloughed basement membrane. Usually, however, YAF had spheroids of yolk (Figs. 22, 24, 27 and 28) of variable size within the follicle. A certain degree of phagocytosis of yolk (Fig. 28) was evident. In some YAF the sprouts of capillaries were observed to grow in such a way that they traversed the thecal and granulosa layers reaching the yolk material (Figs. 26, 27 and 28). Very often such minute capillaries were seen to rupture leading to accumulation of blood around the peripheral yolk spheroids (Figs. 27 and 28) which later migrated towards central parts (Fig. 25a, b). Presumably, this kind of development facilitated a comparatively quick rate of phagocytosis of the yolk contents (Yolk etc.). Removal of yolky matter in such follicles in this manner might lead to a gradual collapse of the follicular wall. Due to such a mode of regression, YAFs at later stages resembled LGAF, and thus, might add to the ovarian complement of this atretic type.

SEASONAL VARIATION IN ATRETIC FOLLICLES:

Seasonal trends in regard of occurrence of atretic follicles are shown in table 2.2. The number of GAFs
increased slowly towards and during the breeding season, reached a peak during egg-laying period and declined thereafter. Frequency of occurrence of LGAP increased significantly ($\chi^2 P < 0.05$) during transition from (1) winter and pursuit periods to nest-building, (2) from nest-building to egg-laying (3) from egg-laying to incubation and (4) from incubation to nestling periods. LGAFs from birds with nestlings and from post-breeding birds differed in histologic characters (reduced cellular vacuolation and decrease in nuclear compression) from LGAFs of earlier periods (winter, pursuits, nest-building, laying and incubation periods). As mentioned earlier, presence of YAF was largely confined to egg-laying, incubation and nestling periods (see table 2.2).

**STROMAL GLANDS:**

Sections of ovaries collected during all the months in this study-period showed presence of stromal glands in varying number and degree of development (Figs. 29 to 32). The stroma of most of the ovaries collected had few clusters and strands of gland cells which were widely scattered in the stromal tissue. Females collected during the mid nest-building stage had ovarian stromata occupied profusely by large lightly stained gland cells. The development of stromal glands was slower during post-
breeding and winter periods but a gradual growth was very much in evidence from pursuit period onwards. A less significant reduction in stromal glands during laying, but it was predominant during incubation period.

DISCUSSION

Seasonal variations in ovarian follicular diameters in Corvus splendens corresponded to those recorded in many other annual breeders (Bissonnette and Zujko, 1936; Peterson, 1955; Johnston, 1956; Barry, 1962; Phillips and van Tienhoven, 1962; Lewin, 1963; King et al., 1966; Lofts et al., 1966; Erpino, 1969; and Hutchison, 1974). Maximum follicular growth was recorded in the last phase of nest-building and during laying period. Follicular regression began immediately after cessation of laying. This short span of peak ovarian activity (less than two and a half weeks) in comparison with longer period of maximum testicular activity (Chapter 1) agrees with observations in California Gull Larus Californicus (Johnston, 1956), Atlantic Brant (Barry, 1962), white crowned sparrow Zonotrichia leucophrys (King et al., 1966), Black billed magpie, Pica pica (Erpino, 1969).
Thecal gland cells, the presumed source of estrogen (Marshall and Coombs, 1957) showed varying degrees of development in correlation with majority of the patterns of behavioral stages. One discrete peak of thecal gland abundance occurred during the mid-nest building stage suggesting an increased production of estrogen. Sexual behaviour and oviducal development (Figs. 2 and 3), both of which are estrogen-induced (van Tienhoven, 1961), occurred two to three weeks after peak development of thecal glands.

In order to discuss the problem of renesting and the possibilities of double broods, if it occurs, in some other regions of India and elsewhere in this species of crows, the average values for clutch size incubation period and rate of laying must be established. An average of 4-5 eggs per clutch has been considered as the normal clutch size for this bird (Corvus splendens). To find out the average size of clutch; data from different sources have also been considered. Four or five eggs were found in a clutch of house crow during this study. In past, different workers have reported different sizes of a clutch for this bird (3 to 6 eggs by Hume (1889-97); 9 eggs by Dewar (1929) and 4-5 eggs by Lamba (1969). The duration of incubation period as reported by others, is less variable than the opinion regarding the size of the
clutch. Lamba's (1969) statement regarding the length of incubation period (16-17 days) matched well with the present observations. It could be said that the Indian house crow has got shorter laying period when compared with the laying period of same birds like California Quail (see Lewin, 1963). Lewin (1963) recorded 14 eggs in a clutch of California Quail, the rate of laying being 1.4 days for each egg and an incubation period of 22 days duration. It may be calculated that on an average it takes 19.6 or about 20 days to complete a clutch and a total of 42 days from the laying of the first egg to the hatching of the brood. Lewin recorded in 1954 (cited from Lewin, 1963) a very long laying period in California Quail and hypothesized that during a laying period of this length there is ample time for renesting even if clutches were destroyed or abandoned in late stages. Considering this account, it is logical to believe that house crow having a shorter laying period may not be able to resort to double brooding (by the same bird) in that season.

Birds have been classified in two general categories according to their pattern of egg-laying (1) Determinate and (2) Indeterminate (Lehrman, 1961). It is also known that the removal, during laying, of eggs from the clutch of an indeterminate layer leads to maturation and ovulation
of additional ova so that the normal "acceptable" clutch size is restored (Lehrman, 1961). It has been mentioned by Lamba (1969) that Indian house crows are indeterminate layers and in this connection wrote: "that the clutch size in indeterminate layers like this bird is conditioned by a number of ecological and physiological factors, details of which can be found in Lack's (1947) paper". In this study on crows Lamba did not seem to have marked the birds in the field under observation, thus it remains equivocal whether the same crows renest and breed twice or part of the population breeds early and the remaining population breeds later in November-December, if favourable environmental factors exist during that period. From the facts cited above it is illogical to believe that the house crow is an indeterminate layer and it renests also to have a second brood.

Studies on house swifts, *Apus apus* and *Apus affinis* (Naik and Naik, 1965a; Naik and Razak, 1967 and Shivnarayan, 1972) have established that the swift populations in Baroda (India) exhibit, two full gonadal peaks in a 12 month period and that is a constant feature for the house swift populations of Baroda. The gonads of breeding birds (house swifts), after every breeding during May to September, undergo a partial regression during
which the testes tend to maintain components from which a spermatogenic apparatus can be rapidly drawn (Shivnarayan, 1972). In this connection Naik and Razack (1967) mentioned that some of the swifts (males), but not all, sustain their gonads in full breeding potency until they breed for the second time. Partial regression favours breeding for the second time with a short lag of time, while complete regression does not. Later view explains, rather more correctly, why crows do not breed or renest. Dilager (1960) observed that more follicles matured than ovulated in determinate laying African parrot (Agapornis sp.), but that atresia of remaining follicles occurred when three to eight eggs were laid. Barry (1962) believed that while a limited number of follicles matured in Atlantic Brant, environmental factors which delayed oviposition induced a flaccid type of atresia (in mature follicles) in which yolk was resorbed. Thus in two of the three nesting seasons, unfavourable weather prevented egg-laying and resulted in atretic loss of over 60% of mature follicles in brants. Therefore, determinate laying in brant and African parrots appears to entail different processes. Otherwise, indeterminate, and not determinate, laying would logically require maturation of more follicles than normally appear in the clutch, since additional ova must
be available to supplement deficient clutches. Observations on the crow ovary during the present study indicated that only ova destined to ovulate attained diameters greater than 15.0 mm. Presumably the determinate laying in house crows involved a mechanism whereby follicular growth to a size approaching only 30-40% of the diameter of ovulable follicles was restricted to ova (maximum n=6) appearing in the clutch. This may indicate that the clutch size was fixed very early - perhaps before the actual laying period. This may be similar to the mechanism in Brants and Black billed Magpies, but appears more efficient than that of African parrot (Agapornis sp.), since energy was not expended on development of excess large follicles. Although pituitary control of egg-laying remains unclear (Duhum and Clapp, 1962), data from the Indian house crows (see Chapter 6) suggest that gonadotropic hormones might act preferentially on those follicles that are destined to ovulate.

Ecological and behavioural studies of renesting in birds include those of McCabe (1963) on Alder Flycatchers, Empidonax traillii; Fankhauser (1964) on Redwinged Blackbirds, Agelains phoeniceus; Gates (1966) on Ring-necked Pheasants, Phasianus colchicus; Andrews (1968) on Jungle Babbler, Turdoides striatus; Naik and Razack (1967, 1968)
and Razack and Naik (1968) on House Swift, *Apus affinis*; Erpino (1969) on Black billed Magpie (*Pica pica*) and Shivnarayan (1972) on House Swift, *Apus apus* and many others. In addition to these above mentioned studies, many other workers have shown the importance of renesting in population maintenance (Stotts and Davis, 1960). Little is known of the physiological processes involved in renesting of other birds in general and Crows in particular. Phillips and van Tienhoven (1962) and Naik and Razack (1967, 1968) reported gonadal correlates of renesting behaviour in Pintails (*Anas acuta*) and Swifts (*Apus apus*) respectively. Barry (1962) presented data on gonadal regression in brants, from which he inferred that the species was physiologically incapable of renesting, while in Magpies, field observations (Erpino, 1968b) of marked birds suggested renesting. This was interpreted as a result of selection against prolongation of nesting in an area with a potentially very short nesting season. This kind of prolongation of nesting was not possible in house crows as in doing so they will have to face unfavourable season (late July and August) of heavy rain and this condition will not favour raising of a second brood or renesting during mid-monsoon. Barry's (1962) suggestion is worth mentioning here. He suggested that short nesting seasons in the Arctic regions acted against renesting in
Atlantic Brant. Lewin's (1963) observations on California Quail support Barry's view of renesting. Physiological correlates of absence of renesting behaviour in female Indian house crows were as follows: The ovary showed no maintenance of many healthy follicles during incubation period. Not only this, but it does not show further growth of existing follicles at that time. It should be mentioned here that testicular regression and degeneration were also observed in the same period (incubation period). The growth of the follicles was resumed once again in nestling period. It is logical to presume that renest clutches may not arise from those follicles which are not actively maintained during incubation. Histologic features of follicular regression, including a reduction in size of healthy follicles, a decrease in mitotic activity in the granulosa, and a general increase in atretic follicles (Table 2.2) observed in the transition from incubation to nestling periods support macroscopic observations suggesting a marked decrease in occurrence of healthy follicles. Aspects of gonadal regression in both sexes, therefore, suggest that physiological constraints act against renesting. Moreover, behavioural interactions between mates (Lehrman, 1961; Brockway, 1965; Brown, 1967) and between birds and
their nests (Hinde, 1965; Lehrman, 1965) will be of major importance in eliciting ovarian maturation in renesting. In this context, Erpino (1969) believes that, renesting, whenever it occurs, its frequency ultimately limited by the males, where complete regression of the testis may have occurred prior to that of the ovary. He explained for example, repeated destruction of nests during incubation could result in prolonging ovarian activity but testicular regression might render males incapable of behavioural responses needed for inducing the necessary ovarian development.

Descriptions of completely atretic follicles presented here agree in general with those observed in the Rook (Marshall and Coombs, 1957) and the Magpie (Erpino, 1969), although, bursting or yolky atresia of intermediate-sized follicles was not reported in the Rook. It is mentioned earlier that bursting-yolky and intermediate-sized atresia were hardly noticed in Indian house crows. Early atresia in the Rook has been described as a process of lipoidal metamorphosis within the ovum where granulosa cells did not dissociate, the cells in the core of atretic follicle which were derived from fibroplasts invade the follicle, become hypertrophied and lipoidal (Marshall and Coombs, 1957). Early atresia in Magpie (Erpino, 1969) differed from that in the Rook but resembled with that of
house crows. Fibroblasts in atretic follicles, however, apparently persisted and formed a partition between the central lipid core and outer thecal layers (Figs. 11, 22). Fibroblasts were neither hypertrophied nor did they increase in number. They are very much less in house crow's ovarian atretic follicles. Central lipoidal cells appeared to stem from the granulosa rather than from fibroblasts or from thecal gland cells as reported by early workers (Brambell, 1956). Atresia in Indian house crow, particularly in early stages, resembled that seen in starlings (Bullough, 1942), Fulmars, Fulmaris glacialis (Wynne Edwards, 1939), Black billed Magpie, Pica pica (Erpino, 1969) and mammals (Ingram, 1962). The fate of lipo-glandular atretic follicles in Rook and Indian house crows differed in late phases but the processes were resembling that found in Magpies. Marshall and Coombs (1957) found that lipoidal AF were short lived and that connective tissue infiltration of AF resulted in obliteration of central lipoidal cells and dispersal of peripheral gland cells into the ovarian stroma. Initial stages of destruction of AF were noted in the beginning of post-breeding phases (August, early September) but intact lipoglandular AFs remained the most conspicuous gland-like ovarian units through the late post-breeding phase
(October). Since winter (November to February) ovaries had few atretic follicles, study of July-August ovaries provided information on regression of completely atretic follicles in general.

Though the site of synthesis of progesterone in the avian ovary remains unclear (van Tiehoven, 1961), lipoidal atretic follicles were proposed as progesterone producing sites in Rooks by Marshall and Coombs (1957). The seasonal incidence of lipo-glandular atretic follicles in house crow paralleled events influenced by progesterone in some sps. These include oviducal development (Brant and Malbandov, 1956) incubation behaviour (Lehrman, 1965) and parental nest defense (Vowles and Harwood, 1966). Occurrence of lipo-glandular atretic follicles in house crows differed from that in Magpies, since nesting crows but not magpies, had lipoidal atretic follicles (see Erpino, 1969). Frequency of lipoidal AF declined after the breeding season in Rooks, while it declines after post-breeding in Indian house crows and Magpies. In this connection Erpino's suggestion stands true that the possible endocrine role of atretic ovarian follicles in birds warrants further attention.

Ovarian stromal glands were observed in starlings by Bullough (1942), in Rooks by Marshall and Coombs (1957)
and in Black-billed Magpie by Erpino (1969). Origin of stromal glands i.e. from (1) stromal fibroblasts and (2) cells of atretic follicles which have been dispersed through connective tissue - was proposed by Marshall and Coombs (1957). In Rooks, Marshall and Coombs (1957) observed a tremendous increase in stromal glands during two to three weeks before oviposition and intense sexual behaviour; but in Indian house crows such an increase in stromal gland development was observed from the time of nest-building period, which declined to a more or less resting state before incubation period, thus, a peak in stromal gland development lasted comparatively longer (as it began earlier) in house crows than what is observed for Rook. Magpies (see Erpino, 1969) differ from Rook as well as house crows in this regard as a high peak which was recorded in nest-building period apparently declined to a resting state before development of the oviduct and vigorous sexual behaviour just prior to laying period. It could be said that in Rooks as well as house crows, destruction of lipo-glandular atretic follicles could provide stromal glands during laying period. The high peak in stromal gland development during nest-building period in house crows may probably originate directly from connective tissue elements as the frequency of
occurrence of atretic follicles during this period of nest-building was low. Erpino (1969) believes that in *Pica pica*, the stromal glands originate from connective tissue precursors during nest-building period. He correlated the stromal gland cells which originated from fibroblasts as homologous to Leydig cells of testes and suggested to be androgenic (see Marshall and Coombs, 1957); while gland cells of follicular origin were believed to be estrogenic (see Marshall and Coombs, 1957; Erpino, 1969). It is worth to make a mention here, that histochemical evidence of androgen secretion by stromal glands in the fowl was reported by Wood and Domm (1966). Oviducal features exhibited development along with the growth of the healthy ovarian follicles during the annual cycle, which implies that the follicular source of sex hormones is manifested in this way.
EXPLANATION TO FIGURES

Microphotographs revealing morphological and histological features of the ovary of Corvus splendens.

PLATE I

Fig. 1. Regressed ovarian condition as evident in the month of September. X 10 and X 125.

Fig. 2. A section of regressed ovary from September, showing numerous smaller ovarian follicles X 125.

Fig. 3. Appearance of the ovary in the month of March. The adjoining section reveals some degree of ovarian & follicular development met within the end of pre-breeding period. X 8 and X 28.

Fig. 4. An ovary from Late May (Nest completing period). Section shows many medium sized and few enlarged follicles along with the smaller follicles. Proportionately medium sized follicles increase by this time but do not reach the ovulable size. X 4 and X 28.

Fig. 4a. Showing comparative morphological changes of the oviducts (from left to right side of photographs) corresponding with the ovarian development shown in figs. 1, 2 and 3 respectively. X 1
Plate: II

Fig. 5. Ovary from June (breeding period). Out of many medium sized follicles, only few (two are visible in photomicrograph) attain ovaluable size just prior to evaluation. Note the rich supply of blood to the enlarged follicles and the poorly vascularized stigma. X 2

Fig. 6. Post ovulatory follicles (P - OF, Black arrows) (Mid-July) in early stage i.e. just after the ovulation has occurred and have flattened due to the collapsed wall. Also note the atretic follicles (AF - White arrows). X 2.

Fig. 7. Post-ovulatory follicles (black arrows) in Mid-stage of resorption. Reduction in size is clearly evident due to their resorption. Also note the atretic follicles (White arrows). X 2.

Fig. 8. Post-ovulatory follicles (P.OF.) (Late July). One P. - OF. is in an early stage (↑) and two crumpled P. OFs. (†) in terminal stage of resorption are seen. The latter have resorption to such an extent that they have become indistinct. Note one big yolky atretic follicle (YE) attached thro' a pedicle (↑) and smaller atretic follicles (AF, White arrows). X 2.
Fig. 8a. Oviduct from a crow (laying period). Note an egg in the oviduct. X0·25

PLATE III

Fig. 9. A healthy follicle having well developed granulosa layer (G) thecal layer (T) and the germinal vesicle (Y). X 52.

Fig. 10. Wall of a healthy follicle in early stages of development showing less developed thecal gland cells (T) and the granulosa layer (G) having two to three cells' thickness. X 125.

Fig. 11. Wall of a healthy follicle, showing developing thecal gland cells (T) and the granulosa layer (G) having three to four cells in thickness. X 125.

Fig. 12. Wall of the healthy full grown follicle revealing very well developed thecal gland cells (T) and granulosa layer (G) having two to three cells' thickness. Compare with Fig. 10 & 11 for noting differential thecal gland cell development—granulosa layer maintaining the level already attained of the stage depicted in Fig. 11. X 125.

Fig. 13. A part of the follicular wall of a large, yolky atretic follicle (YAF). Note highly lipoidal
granulosa cells (G), abundance of yolk platelets, inner thecal gland cells (IN) and a thick outer thecal layer (OT). X 125.

Fig. 14. Portion of yolk atretic follicle, in advanced stage, characterized by dissolution of granulosa cells and larger but reduced number of yolk platelets (YG). Granulosa cells (G) get destroyed and the inner thecal layer (IN) is lined internally as well as externally by linearly arranged fibroblasts (F). X 125.

Fig. 15. Yolky atretic follicle showing a distinct type of structure. The basement membrane, which remains attached to granulosa layer, is seen detached from thecal layer and shows a complex folded pattern. The granulosa cells (G) show lipoidal and vaculated appearance. Also note highly lipoidal nature of both the inner (IN) as well as outer (OT) thecal layers. X 125.

Fig. 16. A magnified view to show a folded granulosa layer of yolky atretic follicle. X 115.
PLATE : IV

Fig. 17. Single lipo-glandular atretic follicle (LGAF), in early stage of atresia. Inner (IN) and outer (OT) thecal gland cells and granulosa cells (G) are clearly visible. Granulosa cells have shifted to central position and are reduced in number. Fibroblasts and macrophages are noticed between granulosa and inner - thecal layer. X 52.

Fig. 18. A LGAF in advanced stage (mid-stage) of atresia. Due to proliferation and inward movement of inner thecal cells (IN), granulosa cells (G) occupy the diminishing central area and are partitioned off from thecal gland cells (T) by fibroblasts (F). The granulosa cells are highly lipoidal and show shrunken, eccentric nuclei. Central thecal gland cells are also heavily lipoidal. X 52.

Fig. 19. A LGAF in the final stage of atresia. No more granulosa cells are visible. Inner thecal glands cells proliferate and collapse. Note a slight reduction in the outer thecal layer. Fibroblasts, macrophages and other connecting tissue elements are sandwiched between collapsed thecal wall. X 52.

Fig. 20. Terminal stage of atresia. The rarity with which this stage was encountered suggests a rapid transition from previous stages of glandular
atresia to lipo-glandular atresia. X52

Fig. 21. Single follicle undergoing glandular atresia (GAF)
Note inward proliferation of granulosa cells from the peripheral region. These cells (G) show darkly stained nuclei which are more or less round or oval. The basement membrane - inner to thecal gland cells (T) - is indistinct. X 52.

Fig. 22. Magnified portion of micrograph: 13, showing details of granulosa cells (G) and the thecal elements (T). X 200.

Fig. 23. and 24. Advanced stages of GAFs vaculation and steatogenesis of granulosa cells (G) is pronounced and phagocytes are in abundance. Innermost thecal gland cells are also lipoidal. X 125.

PLATE: V

Fig. 25. Yolky atretic follicles: Note in (a) blood accumulation in initial stages in peripheral region forming smaller pools (BP) and in (b) bigger size of blood pools (BP’), as smaller pools merge and progress towards more central area of follicle in an advanced atretic stage. X 52.

Fig. 26. Wall of yolku atretic follicle showing growth of minute blood vessels (BV) which traverse the thecal layers (IN, CT) and the granulosa layer (G). X 200.
Fig. 27. Portion of yolky atretic follicle showing ruptured sprouts of capillaries after traversing thecal and granulosa layers so that blood cells get mixed up with yolk forming blood pools (BP). X 125.

Fig. 28. Showing growing sprouts of blood capillary (BC). Yolk-platelets, phagocytes and macrophages can be noticed around them. X 125.

Fig. 29. Showing minimal development of stromal glandular components during pre-breeding (winter) period. X 125.

Fig. 30. Stromal gland cells (S) seen during April— a increase in size and number. X 125.

Fig. 31. Well developed stromal gland cells (S). Maximum development is observable during mid-nest building period. The glandular elements occupy larger areas and become abundant and highly lipoidal in character. X 125.

Fig. 32. Regressing stromal gland cells (3) seen during late laying period (Mid & Late July). X 125.

PLATE: VI

Fig. 33. Wall of a normal post-ovulatory follicle (P.OF) in cross section. Note increased vascularity and prominent thecal layer. X 28.

Fig. 34. Wall of a normal P.- OF- in cross section. Note blood cells (B) and detached granulosa cells(G). only a few granulosa cells remain attached to thecal layers (T). Much of the thickness of (P.- OF) wall consists of thickened thecal layers. X 125.
Fig. 35. Another type of YAF showing intrastromal rupture of thecal layers. Large yolk platelets are abundant. Lipoidal granulosa cells and yolky platelets are seen moving outward, through the rupture in thecal layers. X 125.

Fig. 36a. to 36c. Photomicrographs yolky atretic follicles which are shrunken. These follicles were more common during the months of August and September. X52