REPRODUCTIVE CYCLE OF THE MALLARD DUCK

By Oscar W. Johnson

Considerable work has been done on the behavioral patterns associated with the reproductive cycle of waterfowl. The books by Sowls (1955) and Hochbaum (1959), and the papers by Ramsey (1956) and Johnsgard (1960) are notable in this regard. There has been, however, very little research on the gonadal changes associated with the cycle. With this in mind, a study was undertaken in southeastern Washington the main objective of which was to trace the cyclic changes of the reproductive organs of the Mallard (*Anas platyrhynchos*).

METHODS

Wild Mallards (81 males and 57 females) were collected from March, 1958, through June, 1959. Five additional males were taken in May of 1960. An effort was made to record the undisturbed behavioral actions of each specimen immediately prior to collection. Such notes helped greatly in later categorization. The desired tissues were excised in the field and fixed in AFA solution (glacial acetic acid, 10 parts; 37 per cent formalin, 10 parts; 95 per cent alcohol, 30 parts; and distilled water, 50 parts). All collected materials were brought back to the laboratory for examination and the recording of various data. The laboratory procedures were as follows:

Males.—Testicular length and width (measured in the dorso-ventral plane) in millimeters were obtained with a vernier caliper. The testes used for microscopic analyses were dehydrated in dioxane and embedded in paraffin. The preparations were stained with Heidenhain's hematoxylin and counterstained lightly in eosin.

The penis was removed by cutting along its lines of attachment flush with the cloacal wall. This procedure was simplified by pressure eversion of the penis through the cloacal opening at the time of collection. After removal the penis was weighed. It was found that penis weight was a much better relative measurement than length.

Females.—The largest follicle on each ovary was measured in millimeters using the vernier caliper. Measurements were made in the same plane as the stigma. Oviduct length (to the nearest five millimeters) was measured by cutting the supporting ligaments (which tend to keep the structure in a convoluted position), and then gently straightening the tube along a millimeter rule.

Both sexes.—Bursae were dissected away from the cloacae, and their maximum outside length measured with a millimeter rule. Diameter measurements were made with a vernier caliper near the middle of each bursa. All excised structures, after having been carefully dissected away from extraneous tissues, were weighed to .001 gm. on a chain balance. Weighings were made in a sealed jar containing a piece of filter paper saturated with alcohol. This method minimized the degree of error from evaporation. The weight of the jar was standardized after every other weighing to maintain a high degree of accuracy. The feather development of each specimen was closely inspected. Plumage data were valuable in categorizing birds during later analyses.

BURSA OF FABRICIUS

In juvenal Mallards, the bursa is a conspicuous, glandular organ with a well developed lumen. On the basis of bursae which were examined from flightless young, it appears that the size of the structure in Mallards is maximum at about the time flight is achieved. The mean bursal measurements for nine juveniles (males and females capable of flight) taken during July and August are as follows: length, 32.1 mm.; diameter, 8.0 mm.; and weight, 1.54 gm.

Much reduced remnant bursae were found in birds collected during the winter and spring of 1959. The retention of these remnant structures was not realized early in this study, and undoubtedly some remnant bursae were overlooked during the spring and summer of 1958. These reduced structures appear as slender, flattened pieces of tissue, and have no apparent lumen. Their occurrence poses an important question. Are remnant bursae strictly characteristic of yearling birds, or may such structures be retained indefinitely? It is possible that careful dissection would disclose the general retention of remnant bursae in adult Mallards. It is obvious that knowledge of the later regressive stages in bursae of Mallards and other waterfowl is inadequate. Work under controlled conditions is needed to clarify these details.

After the bursae of Mallards regress to a weight level of about 0.10 gm., they appear to persist with little change for an indefinite period. The mean measurements of 25 remnant bursae taken from late January through May are: length, 16.8 mm.; diameter, 2.0 mm.; and weight, 0.07 gm.

Among males, remnant bursae reached a very inconspicuous size by January 31, 1959. Hence in analyses, males taken after this date were considered adults. In females, birds of yearling status seemed obvious until February 22. Females containing very reduced bursae collected after the latter date were considered as adults.

MALE REPRODUCTIVE SYSTEM

Testes

Spermatogenesis

The following classification was developed to express the relative histological development in the testes of male Mallards taken throughout the annual cycle. Essentially these stages are a modification of those given by Johnston (1956).

Stage 1.—(Inactive condition—tubular lumina contain spermatogonia and a few primary spermatocytes; fig. 1a). Each tubule shows a peripheral row of spermatogonia. Most tubules also contain primary spermatocytes, which vary from merely a few individuals to one irregular row in some tubules. Primary spermatocytes may be wedged in toward the basal spermatogonia or lie toward the lumen well within the peripheral spermatogonia. A very few primary spermatocytes in synapsis are occasionally found. Most tubules show a small central lumen, which is generally bordered by considerable amounts of clear cytoplasmic material. Toward the end of this stage, primary spermatocytes tend to become more abundant and move closer to the lumen, and the cytoplasmic border becomes less apparent.

Stage 2.—(Increase in the number of primary spermatocytes, many of which are in synapsis, fig. 1b). An increase in both spermatogonia and primary spermatocytes is apparent. During early phases of Stage 2 (the initiation of recrudescence) primary spermatocytes in synapsis are found in scattered clumps throughout the section. During later phases, from one-fourth to one-half of all primary spermatocytes in a given field are in synapsis. Some tubules possess a lumen, but most tubules are filled with cells and the lumina as well as their clear cytoplasmic borders are obliterated.

Stage 3.—(Majority of primary spermatocytes in synapsis, and a few secondary spermatocytes present). Most tubules show one or two rows of spermatogonia and two or three rows of primary spermatocytes. Only a very few of the latter are not in synapsis. Some tubules show a few secondary spermatocytes. A few tubules possess a small lumen—most appear completely filled by the rapidly developing cells.

Stage 4.—(Secondary spermatocytes, some spermatids and immature spermatozoa, fig. 1c). Tubules generally show two rows of spermatogonia, with two or three rows of primary spermatocytes in synapsis. The central portions of most tubules have irregularly placed secondary spermatocytes and spermatids undergoing spermiogenesis. Few to moderate numbers of maturing spermatozoa can be found in many of the central areas of the tubules. All spermatozoa are immature and only a very few are attaching to Sertoli cells. There are no distinct open lumina—the tubules are filled with developing cells.

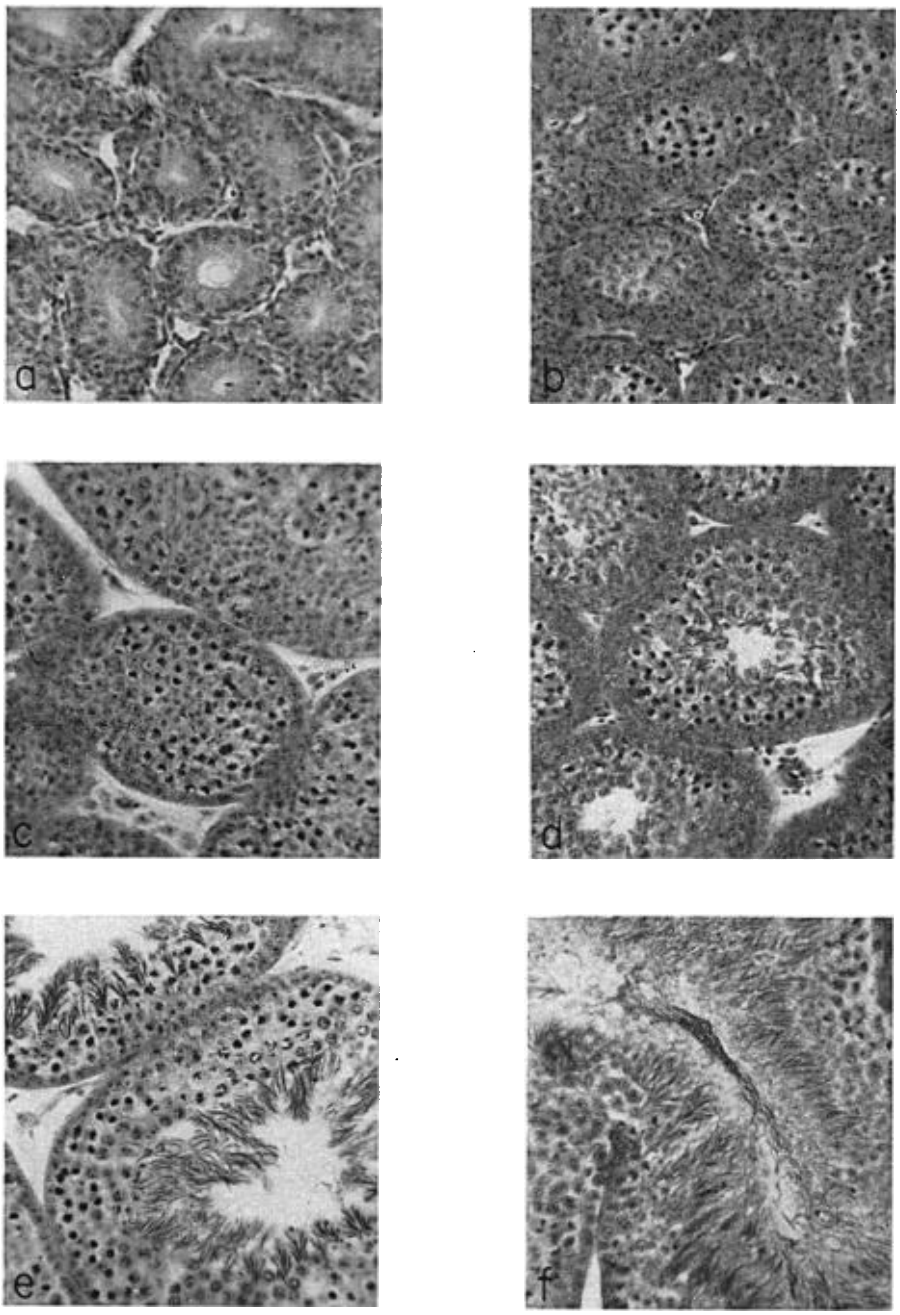

Fig. 1. Photomicrographs of testes of Mallards (*Anas platyrhynchos*) showing representative histologic stages. a, Stage 1; b, Stage 2; c, Stage 4; d, Stage 5; e, Stage 6; f, Stage 7. All photographs are approximately 240 ×.

Stage 5.—(Large numbers of spermatids, and moderate numbers of spermatozoa, fig. 1d). Many spermatids showing various degrees of the spermiogenetic process are present. Many maturing spermatozoa are leaving central tubule areas and moving peripherally for attachment to Sertoli cells. Open tubular lumina, although small, are now becoming quite common. Some tubules contain well developed bundles of sperm attached to Sertoli cells. The first mature spermatozoa are apparently produced during this stage.

Stage 6.—(Full breeding condition, fig. 1e). Testes in this stage show maximum size, weight, and tubule diameter. Large numbers of maturing spermatozoa are grouped in regular bundles attached to Sertoli cells distributed around the course of each tubule. A few spermatozoa are present in the lumina of the tubules and probably represent mature sperm in the process of transit through the tubules to the duct system. Almost all tubules show a large central lumen.

Stage 7.—(Regression, fig. 1f). The first indication of regression is the casting off of large numbers of spermatozoa into the tubular lumina. From this point on, the other epithelial contents of the tubules are sloughed in order, and the tubules are filled with detritus and degenerating cells. During late periods of this stage, tubules contain small numbers of primary and secondary spermatocytes along with cellular detritus.

TABLE 1

SUMMARY OF REPRODUCTIVE DATA FROM 86 MALE MALLARDS

Number of specimens	Range in testis weight (av. of right and left) in gms.	Distribution of spermatogenic stages	Range in penis weight in grams	Collection period
		Pre-breeding males—Paired but not yet sexually mature		
20	.075–4.940	1(1), 2(8), 3(4), 4(5), 5(2)	.289–2.946	2/21 to 4/6/58 11/24/58 to 4/4/59
		Mature breeding males—Paired and sexually mature		
11	3.270–15.844	6(11)	1.295–3.602	3/22 to 5/11/58 3/21 to 4/26/59
		Early desertion drakes—Show no evidence of postnuptial molt		
6	4.491–15.994	6(6)	1.740–2.780	4/12 to 4/27/58 4/12 to 4/26/59 and May, 1960
		Drakes undergoing postnuptial (eclipse) molt		
11	.086–8.632	6(3), 7(8)	.422–2.480	5/11 to 7/12/58 and May, 1960
		Drakes undergoing prenuptial molt		
8	.076–.211	1(4), 7(4)	.415–1.273	8/3 to 10/16/58
		Adult drakes (winter)—Full plumage, not paired		
10	.077–.439	1(4), 2(5) 3(1)	.310–1.307	11/13/58 to 3/15/59
		Immature drakes (summer)—All in early prenuptial molt		
4	.023–.043	1(4)	.010–.021	7/26 to 8/17/58
		Immature drakes (fall)—Prenuptial molt well advanced		
2	.048–.068	1(2)	.026–.039	9/28 to 10/24/58
		Immature drakes (winter)—Prenuptial molt complete, not paired		
14	.040–.127	1(6), 2(8)	.010–.876	11/23/58 to 1/31/59

Table 1 summarizes reproductive data for males. We may first note the distribution of the histologic stages of spermatogenesis with regard to the various categories into which the birds have been grouped.

Stage 6 (full maturity) is representative of paired breeding males. It is also found

in males which have recently deserted breeding territories and are in a transitional period between breeding and the postnuptial molt. In some birds, full maturity of the gonads tends to persist into the early stages of the postnuptial molt.

Regression (Stage 7) is a rather lengthy process which begins early in the period of postnuptial molt and persists in most birds well into the prenuptial molt period *during the fall* when the breeding plummage is again assumed.

Complete regression to Stage 1 occurs during the prenuptial (second fall) molt period. All testes appear to be fully regressed by the time that complete new prenuptial plumage is acquired. Stage 1 persists through most of the wintering period, and much courtship and pair formation is completed during this time of gonadal quiescence. Observations of wintering Mallards along the Snake River near Clarkston, Washington, disclosed sexual display and pair formation from early October onward. By late December and early January (the time of general male recrudescence) approximately 35 to 40 per cent of the males present were already paired.

The transitory stages (2, 3, 4, and 5) between inactive condition and complete recrudescence occur from midwinter through early spring. During these spermatogenic stages, males are generally mated and in a pre-breeding status.

Weight and Size Relationships

This analysis of testicular weight is based upon the mean weight of both testes in each specimen. The general practice in avian studies has been to use figures from just the left testis or from the larger of the two testes. It would seem that the mean weight more accurately denotes the reproductive condition of a given individual.

Table 2 gives a summary of testis weight and size relative to spermatogenic stages 1 through 6. Stage 7 is not included since it seems relatively meaningless to present calculations for the period of regression. The table is based upon adult birds and possible yearling birds which were taken after January 31, 1959 (see section on the bursa of Fabricius).

Table 2

Weight of Testes and Penises and Size Measurements of Testes Relative to Spermatogenic Stages

	Stage number					
	1 (9)[1]	2 (13)	3 (5)	4 (5)	5 (2)	6 (20)
Testis weight (gm.)						
Mean	0.109	0.154	0.520	1.967	3.970	8.234
Maximum	0.148	0.390	1.010	3.707	4.940	15.994
Minimum	0.077	0.075	0.218	0.975	3.000	3.270
Testis size (mm.)						
Mean length	10.44	11.57	17.29	25.84	33.02	41.48
Mean width	3.83	4.43	7.07	10.94	14.02	17.59
Max. length	11.70	15.15	22.85	31.70	33.80	51.70
Min. length	8.95	9.95	13.05	17.80	32.25	31.10
Max. width	4.45	6.37	8.90	15.35	15.00	23.45
Min. width	3.40	3.20	5.45	8.60	13.05	14.15
Penis weight (gm.)						
Mean	0.728	0.825	1.491	1.969	2.183	2.326
Maximum	1.273	1.598	1.911	2.946	2.840	3.602
Minimum	0.428	0.289	0.977	1.448	1.527	1.295

[1] Number of specimens available in each stage.

The general pattern of cyclic change in testis weight and size is evidenced by the means in the table. It is obvious that considerable overlap occurs between maximum and minimum figures. This overlap makes it impractical to attempt to ascertain the histologic condition of testes of Mallards on the basis of weight or size.

If the maximum and minimum weights in Stage 6 are considered relative to the mean value of Stage 1, a range of weight increase from about 30 to 146 times is indicated. One explanation for this range of individual variation might be the length of time that a particular male remains mated and territorial. A lengthy period of territoriality may allow continuing gonadal hypertrophy. The territorial period undoubtedly varies since nest destruction or desertion may cause the hen to start more than one nest. Another influencing factor may be the age of the bird. The lack of suitable techniques to determine accurately the age of waterfowl, and incomplete knowledge of the later regressive changes of the bursa, make it impossible to analyze this matter. It is noteworthy that a bursal remnant was found in a specimen with extremely large testes (mean weight, 15.8 gm.). Johnston (1956) showed definite testicular size differences in various age classes of California Gulls (*Larus californicus*). Wright and Wright (1944) demonstrated that the testes of year-old Redwinged Blackbirds (*Agelaius phoeniceus*) reached only two-thirds the size of adult organs. The need for work under controlled conditions with the waterfowl group is obvious. Höhn (1947) presents data which also indicate considerable weight variation in testes of Mallards of comparable histologic development.

Aside from the possible effects of the total period of sexual stimulation on males in Stage 6, it would also appear that the range in values throughout the spermatogenic cycle is greatly influenced by the present method of assigning rather broad stages to the spermatogenic process. Perhaps a more quantitative technique in arriving at histological considerations would lessen much of this variation.

It is informative to compare the gonad weights of regressed adults with those of immature birds. During the late summer, fall, and winter (August through December) the mean gonad weight for 16 regressed adults was 0.12 gm. During the corresponding period, the mean for 14 immature birds was 0.06 gm. There were no instances of overlap between maximum immature weights and minimum mature weights. By January, however, it appears that at least some yearling males contain gonads of a size comparable to that of adults. In a small sample of two adults and three immatures taken in January, one immature bird overlapped broadly with the adult values.

The weight difference found between the testes of adult and immature Mallards is similar to findings in other birds. Blanchard (1941) and Blanchard and Erickson (1949) report the same tendency in the testes of White-crowned Sparrows (*Zonotrichia leucophrys*). Kirschbaum and Ringoen (1936) found adult House Sparrows (*Passer domesticus*) to have larger testes than juveniles during the fall period. Wright and Wright (1944) found testes of adult Redwinged Blackbirds to be larger than testes of immature individuals throughout the quiescent period.

In most species of birds, the left testis is larger than the right. Mallards appear to deviate considerably from this general rule. Of 82 males in which the weights of both testes were obtained, there were 32 (39 per cent) in which the left testis was larger; 49 (59.7 per cent) in which the right testis was larger; and one (1.3 per cent) in which both testes were equal in weight.

Recrudescence

A great deal of variability in the maturity of testes was encountered during the recrudescent period in the late winter and spring. Such a phenomenon is probably to be

expected in a far-ranging migratory species like the Mallard. Birds collected in southeastern Washington may be representative of different wintering conditions along the flyway (varied light intensities, and so on), and as a result show varied levels of sexual development.

It is also possible that the variation is to some degree induced by racial affinities. Wolfson (1942) showed a differential pattern of recrudescent development in juncos (*Junco oreganus*). He notes that migrant races are later in recrudescence, and that they tend to maintain the intermediate histologic stages of spermatogenesis for longer periods than nonmigratory juncos. Mallards that winter in this area may represent a fairly sedentary population, and hence might undergo recrudescence faster than birds destined to migrate for long distances before breeding.

Another factor which may cause variability in recrudescence is the possible influence of relative age. Wright and Wright (1944) found immature male Redwinged Blackbirds to be about three weeks behind the recrudescence of mature birds. Blanchard and Erickson (1949) found a tendency for the testes of immature White-crowned Sparrows to be of smaller size than those of adults, but there was no apparent difference as to the time of attainment of the various histologic stages of spermatogenesis. As previously discussed, the testes of immature Mallards are smaller than regressed mature testes. The differences, which appear to become much reduced by January, do not seem great enough to add much to the variability in recrudescent development. Also, as table 1 shows, recrudescence appears to begin at about the same time among both mature and immature birds.

The earliest indications of recrudescence (Stage 2 testes) were found in two males (one adult, one immature) both taken on December 11, 1958. General recrudescence among both immature and mature males appears to be underway by late December to early January in this region. If we assume that birds destined to nest in this area (the sedentary population) begin to recrudesce during this time, then a period of about three months is involved before full maturity is achieved in mid- to late March. Males beginning to regress (Stage 7) were found by mid-May, with increasing numbers present during early June. It thus appears that an individual drake may possess full sexual capacity for about 1.5 to 2.5 months.

Regression

The postnuptial or eclipse molt furnishes a time scale with which one can approximate the rate of testicular regression. The important characteristics of the molt according to Hochbaum (1959) are as follows: the assumption of postnuptial plumage requires two or three weeks, during which time the molt is confined to the body feathers; when full postnuptial body plumage is acquired, a simultaneous molt of all remiges and rectrices occurs, rendering the bird flightless; the growth of new remiges and rectrices requires about 2.5 to 4 weeks, during which time the eclipse plumage is retained; when the growth of new flight feathers is completed, the prenuptial molt begins. A number of males in various stages of postnuptial and early prenuptial molt were collected. The data from these birds are summarized in table 3.

The beginning of regression appears somewhat variable in individual Mallards. In general, the first histologic indications of regression correspond with the early phases of the postnuptial molt during which one finds short, newly emerged eclipse feathers well hidden beneath the prenuptial plumage. There is an undetermined length of time following desertion of the territory during which sexual vigor is maintained. This, plus the fact that some birds retain full sexual capacity in the early stages of the postnuptial molt, may

have important implications in renesting behavior. Höhn (1947) also shows individual variability as to the start of regression during the early eclipse period. Seligmann and Shattock (1914) mention drake Mallards which in late spring and early summer still possessed full winter plumage while their testes were considerably regressed. Nothing of this sort was found in the present study, and it may be that the semi-domestication of the Mallards which these investigators were using introduced this variation.

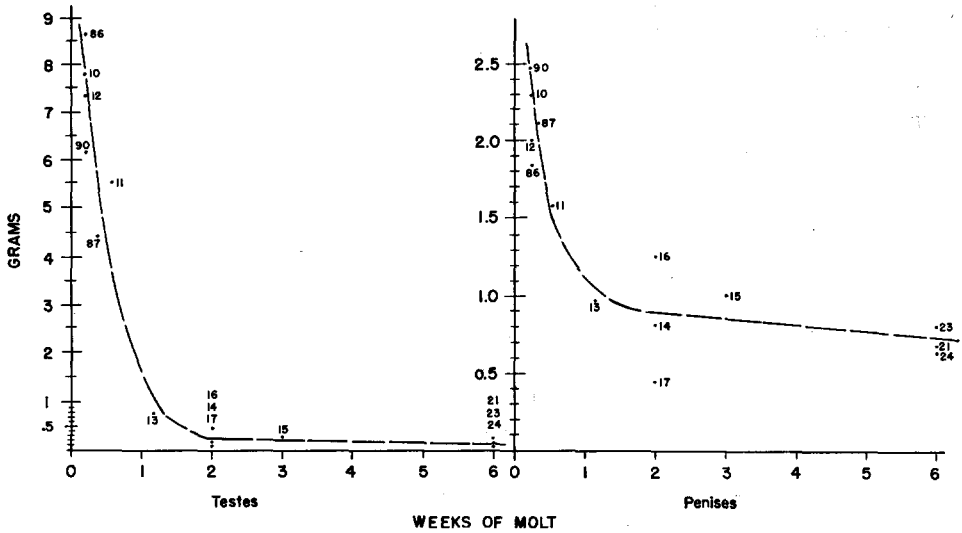

Fig. 2. Approximate weight regression of testes and penises of Mallards. Numerals refer to specimen numbers.

The data from table 3 can be plotted graphically as shown in figure 2. It appears from the graph that the regression of the testes of Mallards is a two-stage process. The first regressive change is fairly rapid. In the first 1.5 to 2.5 weeks of the postnuptial molt, the major part of regression is completed. Following this rapid initial regression, testis weights decrease very gradually into the time of prenuptial molt. This second phase appears to last for one to two months. The considerable time involved in testis regression of Mallards is also indicated by Höhn (1947) who collected males in almost complete prenuptial plumage which still showed histological indications of regression.

Penis

The penis was found to undergo a cyclic change in weight paralleling the testicular cycle (table 2). Penis regression is similar to the two-stage process described for testicular regression. Data are summarized in table 3 and in figure 2.

The size of the juvenal penis remains almost constant for the first several months of the bird's life. Hochbaum (1942) states that the immature penis may remain little changed for from five to ten months. He notes that a few young Mallard drakes may assume the adult penis by mid-November, but that the majority do not reach this point until after the end of December. The first enlarging juvenal penises which I observed were found in late December. Considerable variation was found in penis weight after the first few enlarging organs were noted. Some birds appear to retain juvenal-sized penises into January, and perhaps even later. These variations probably reflect the span of the previous year's hatching season and the consequent relative age of the birds.

TABLE 3

COMPARATIVE ASPECTS OF REGRESSING TESTES AND PENISES IN BIRDS UNDERGOING THE POSTNUPTIAL AND EARLY PRENUPTIAL MOLTS

	Specimen number	Mean testis weight (gm.)	Spermatogenic stage	Penis weight (gm.)
Early stages of eclipse,	10	7.740	6	2.294
postnuptial feathers	11	5.511	7	1.575
5 to 20 mm. long and	12	7.370	6	1.994
completely hidden beneath	86	8.632	7	1.820
prenuptial plumage	87	4.406	7	2.100
	90[1]	6.140	6	2.482
Prenuptial plumage mottled with eclipse feathers	13	0.766	7	0.979
Complete postnuptial	14	0.179	7	0.808
plumage, wing and tail	16	0.508	7	1.246
feathers not yet cast	17	0.086	7	0.422
Complete postnuptial plumage, wing and tail feathers cast, growing stubs very short	15	0.248	7	0.999
Plumage dominantly of eclipse				
feathers, wing and tail feathers	21	0.211	7	0.673
completely replaced, prenuptial	23	0.108	1	0.797
molt just beginning	24	0.090	7	0.623

[1] Right testis damaged, weight applies to left testis only.

The penis of breeding birds is a very prominent, tapering, spiralled (corkscrew-like) structure. The surface is coarsely ridged with flaps of tissue which originate at each side of an external groove and extend transversely around the circumference of the organ. In many adult penises, the transverse ridges are tinged slightly with gray. Except for this variation, the penis is predominantly white. The morphological appearance of the penis changes markedly during regression and recrudescence. The regressed penis is only one-third to one-half the length of the mature organ and is much reduced in diameter. The transverse ridges become much lower, and the whole organ assumes a smooth, white, very slender appearance.

FEMALE REPRODUCTIVE SYSTEM

Cyclic weight and morphological changes.—Table 4 summarizes data for females categorized on the basis of various stages in the annual cycle. Average figures show about a 100 to 1 relationship between the weight of recrudescent and regressed ovaries. When the variation among mature ovaries is considered, a range of about 85–120 to 1 is indicated. The period of time during which a female remains sexually stimulated appears to be an important variable factor. The maximum mature weight shown in table 4 represents the ovary of a bird which had ovulated at least 11 times. The minimum mature weight represents a bird which had ovulated but once. Relative age may have some possible influence on the degree of hypertrophy.

The immature ovary is a flat, inconspicuous organ which is commonly around 15 mm. in length, 5 mm. in width, and 1 to 2 mm. thick. The mean weight of five immature ovaries taken during summer was 0.083 gm. The surface is fissured with fine convolutions and shows no evidence of follicle enlargement. Gradual growth of follicles begins sometime during early fall. By late November the ovaries of most immature hens con-

TABLE 4

WEIGHTS OF OVARIES AND OVIDUCTS AND MEASUREMENTS OF FOLLICLES AND OVIDUCTS FROM ADULT FEMALE MALLARDS AT VARIOUS LEVELS OF SEXUAL DEVELOPMENT[1]

Ovary weight (gm.) and follicle measurements (mm.)	Mature (2)[2]	Gravid (5)	Intermediate (10)	Early (2)	Wintering (6)
Mean	21.888	11.392	2.235	0.682	0.213
Maximum	25.687	14.572	4.626	0.897	0.281
Minimum	18.090	8.257	0.696	0.468	0.146
Largest follicles (range in mm.)	20 to 30	21.6 to 26.5	6.2 to 17.3	5 to 6	1.5 to 3.2
Oviduct weight (gm.)					
Mean	39.075[3]	19.468	6.131	1.448	0.743
Maximum	62.560	26.525	13.828	1.914	0.993
Minimum	21.350	15.402	2.557	0.983	0.459
Oviduct length (mm.)					
Mean	342[3]	259	148	95	90
Maximum	420	300	190	105	110
Minimum	245	210	100	85	85

[1] Mature—laying hens; Gravid—not yet laying, but nearing maturity on the basis of large follicles; Intermediate—weight relatively low, follicles 6.2 to 17.3 mm. in diameter; Early—only slight weight increase from the winter level, follicles 5 to 6 mm. in diameter; Wintering—quiescent organs low in weight, follicles 1.5 to 3.2 mm. in diameter.

[2] Number of specimens available in each category.

[3] Mature oviduct figures are based on three oviducts.

tain follicles of approximately the same size as those of regressed mature birds. After follicle enlargement begins there are no apparent macroscopic differences between mature and immature ovaries. With follicle enlargement the mean weight of immature ovaries increases considerably from summer levels. Nine such organs taken from late November to late February showed a mean of 0.202 gm. This figure is similar to the mean ovary weight for wintering adults (0.213 gm.) as given in table 4.

The oviduct of both gravid and laying hens is a long, highly convoluted, muscular structure. The regressed oviduct becomes flat and ribbon-like, with the exception of the vaginal area which retains a thicker, more muscular appearance. On the basis of the mature and wintering categories in table 4, the fluctuation in oviduct length appears to be about four to one.

Cyclic weight changes of the oviduct indicate about a 52 to 1 relationship between mature and regressed weight levels, with variations ranging from 28–84 to 1 (table 4). This range is likely dependent upon the same factors which influence the range in weight of the ovary. Individual oviduct weights were correlated with the approximate number of ovulations in the way previously mentioned for ovaries.

Immature oviducts are considerably smaller than regressed adult oviducts. The mean weight of nine immature oviducts taken from late November to late February was 0.280 gm. This figure contrasts the mean oviduct weight for wintering adults (0.743 gm.) as given in table 4.

Recrudescence.—It is difficult to delimit accurately the period of time involved in female recrudescence. The most complicating factor appears to be migratory movement which brings into the study area birds of varying degrees of development. This point was discussed earlier in the section on male recrudescence.

The recrudescence of females appears to lag behind that of males in most cases.

TABLE 5

MEASUREMENTS OF OVARIES AND OVIDUCTS OF MALLARDS IN REGRESSION

Class of female	Specimen number	Days of regression	Ovary weight (gm.)	Largest follicle (mm.)	Oviduct weight (gm.)	Oviduct length (mm.)
Incubating hens[1]	63	5	0.415[2]	4.7	5.806	140
	7	9	1.232	5.5	4.325	120
	58	11	1.302	7.0	4.184	130
	56	15	0.953	6.1	3.010	105
	62	20	0.352	3.4	2.979	100
Brood hens[3]	16	25	0.236	2.3	2.013	100
	17	25	0.216	1.9	1.488	80
	6	28	0.371	2.6	2.125	80
	8	32	0.505	3.6	1.440	85
	14	32	0.182	2.0	1.474	85
	11	45	0.168	1.6	1.507	90
	10	53	0.246	2.4	1.286	95
	18	57	0.125	1.7	1.334	85
	12	59	0.208	1.8	1.643	90
	13	73	0.182	2.1	1.551	90
	15	88	0.167	1.7	1.031	85

[1] The regressive period of incubating hens was determined by comparison of the embryos with a preserved series of known age, or by incubating the clutch in an electric incubator (total period of incubation assumed to be 23 days).

[2] Although it did not appear damaged, there is a possibility that part of this ovary was lost during collection; the weight does not seem to fit the trend indicated by the other figures.

[3] The regressive period of brood hens was determined by allowing 23 days for incubation, and then adding the age of the brood to this figure. Brood age was estimated by careful analysis of collected young according to the criteria established by Southwick (1953) and by Gollop and Marshall (1954).

One aspect of the time lag can be gathered from 11 instances in which both members of a pair were collected and in which the hen was either intermediate or gravid (table 4) in reproductive development. Among the 11 drakes, five were in full sexual maturity (Stage 6); three were nearing maturity (Stage 5); the remaining three were in stages 2, 3, and 4, respectively. Höhn (1947) found recrudescing male Mallards two to three weeks in advance of females. Both Kirkpatrick (1944) and Hiatt and Fisher (1947) show similar findings with respect to the Ring-necked Pheasant (*Phasianus colchicus*). The timing difference between males and females in the present study appears to be much the same as reported by the above authors. As previously mentioned the general recrudescence of males in this region begins in late December and early January. On this basis, most females probably start recrudescing by mid- to late January. The gradual enlargement of follicles on the immature ovary was discussed earlier. This growth pattern appears to bring the immature ovary to the developmental level of the regressed adult structure by the time that rapid recrudescence gets under way.

It appears that the initial recrudescence to breeding condition is a gradual phenomenon requiring about two months. An amazingly fast recrudescent development can apparently take place subsequent to this first gradual phase. Sowls (1955) shows renesting by two female Pintails (*Anas acuta*) following loss of newly hatched broods. These birds renested in 16 and 18 days, respectively. As will be shown in the next section, the ovaries of these two hens must have been almost completely regressed, and it seems remarkable that they were able to regain sexual capacity in such a relatively short period.

Regression.—Table 5 compiles measurements of ovaries and oviducts from a group of females in which the regressive periods could be accurately estimated. The data from table 5 are graphed in figure 3.

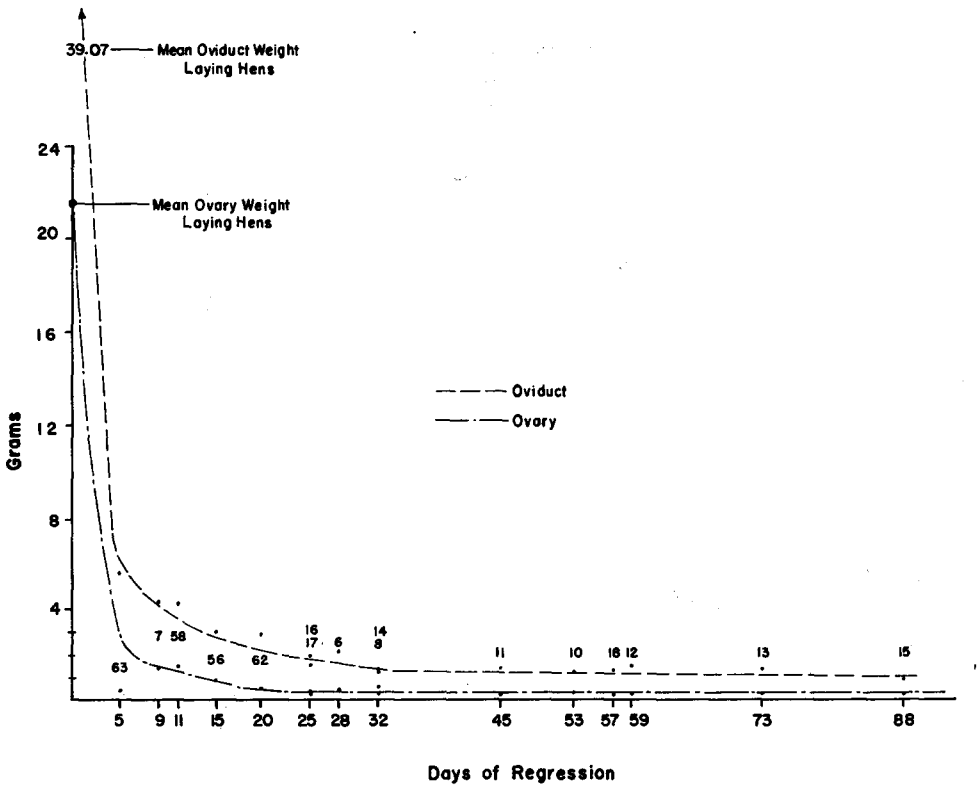

Fig. 3. Weight regression of ovaries and oviducts of Mallards. Numerals refer to specimen numbers.

The close correlation between ovary and oviduct regression, and the exceedingly fast regressive rate during a short period immediately following the start of incubation, are clearly indicated by the graph. In the first five post-incubation days, about 85 to 90 per cent of ovarian regression was completed (allowing slightly higher weight for the five-day ovary), and around 85 per cent of oviducal regression. Meyer, Kabat, and Buss (1947) found that there was very rapid follicle regression in pheasants during the first 36 to 48 hours after incubation began. They report slower regression from the second to the fifth day, and extremely slow regression by the seventh or eighth day. Although they give no figures on total weight of ovaries, it is logical that the trend of follicle regression would be similar to that of weight regression. On this basis, it is very possible that the initial regression in the Mallard is even faster than my data show. At any rate, it is evident that the major part of ovarian and oviducal regression takes place over a very short period immediately after incubation begins.

The time required for complete ovarian regression to winter weight levels (table 4) was varied. Two hens reached such a point after 25 days. By 53 days, all birds appeared to be thoroughly regressed. Considering individual variations, it appears that complete ovarian regression is accomplished in from 25 to 50 days after the onset of incubation.

Weight regression of the oviduct is slower than that of the ovary. Fairly large weight losses are evident during the first 25 to 30 post-incubation days, but after this, losses appear to be very gradual. The 88-day oviduct was approaching complete regression.

It seems likely that at least 100 days are required for regression to the winter level indicated in table 4. Oviduct length does reach winter levels by 25 to 30 post-incubation days, indicating that further weight losses are dependent upon a thinning through continuing resorptive processes.

The regressive pattern of ovary and oviduct resembles that already discussed for testes, in that a two-stage sequence seems evident. The first stage accomplishes the vast majority of regressive change over a relatively short period. The second stage is much more gradual.

SUMMARY

Mallards (*Anas platyrhynchos*) were found to retain remnant bursae. It could not be determined whether these structures are characteristic of yearling birds or are retained indefinitely. Comparative weight and size measurements of both mature and remnant bursae are given.

The testes of 86 Mallards were studied microscopically and placed within a classification consisting of seven histologic stages representative of the entire annual cycle. Histologically mature testes were found in breeding males and also in males which had recently deserted their breeding territories. Some males retain mature gonads during the early stages of the postnuptial molt. The degenerative process of testicular regression begins early in the postnuptial molt period and persists into the prenuptial molt period. The testes appear to be completely regressed by the time that complete prenuptial plumage is acquired.

Testicular weight and size measurements are discussed. A wide range of variation in the measurements of histologically mature testes was found. This may indicate a direct relationship between gonadal hypertrophy and the length of the territorial period. Such a relationship also seems likely for laying females in which greater weight of ovary and oviduct appears to be directly correlated with the number of ovulations, and hence a longer total time of sexual stimulation. Relative age may also be an influencing factor in both sexes.

A great deal of individual variability with respect to sexual maturity was found among both males and females during the recrudescent period. Such variation is probably to be expected as a result of differing environmental conditions on wintering areas; but it may also reflect an inherent phenomenon based on racial affinities, as has been shown for certain passerines. In mated pairs, recrudescence of the female appears generally to lag behind that of the male.

Using events of the postnuptial molt as a time scale, the approximate rate of testicular weight regression was estimated. The overall regressive change appears to be a two-stage process. In the first 1.5 to 2.5 weeks of the postnuptial molt, the major part of regression takes place. Following this, testis weights decrease gradually for a variable period of from one to two months.

The penis was found to undergo a cycle paralleling that of the testes. Weight and morphology changes of the organ are discussed.

It was possible to estimate accurately the regressive periods for a number of females. There is an exceedingly fast regression of both ovary and oviduct during the first few days following the start of incubation. Complete regression of the ovary appears to be accomplished more quickly than that of the oviduct.

ACKNOWLEDGMENTS

I wish to thank Dr. Irven O. Buss for his guidance during the course of this study and for his criticism of the manuscript. Drs. H. L. Eastlick, C. W. McNeil, E. E. Pro-

vost, and G. E. Hudson all offered helpful suggestions at various times. I am very grateful for the financial support given to me by Washington State University.

LITERATURE CITED

Blanchard, B. D.
1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: Environment and annual cycle. Univ. Calif. Publ. Zool., 46:1–177.

Blanchard, B. D., and Erickson, M. M.
1949. The cycle in the Gambel sparrow. Univ. Calif. Publ. Zool., 47:255:317.

Gollop, J. B., and Marshall, W. H.
1954. A guide for aging duck broods in the field. Prepared for the Mississippi Flyway Council Technical Section. 14 pp.

Hiatt, R. W., and Fisher, H. I.
1947. The reproductive cycle of ring-necked pheasants in Montana. Auk, 64:528–548.

Hochbaum, H. A.
1942. Sex and age determination of waterfowl by cloacal examination. Trans. N. Amer. Wildl. Conf., 7:299–307.
1959. The canvasback on a prairie marsh. Second ed. (Stackpole Co., Harrisburg, Pa.).

Höhn, E. O.
1947. Sexual behavior and seasonal changes in the gonads and adrenals of the mallard. Proc. Zool. Soc. London, 117:281–304.

Johnsgard, P. A.
1960. A quantitative study of sexual behavior of mallards and black ducks. Wilson Bull., 72:133–155.

Johnston, D. W.
1956. The annual reproductive cycle of the California gull. I. Criteria of age and the testis cycle. Condor, 58:134–162.

Kirkpatrick, C. M.
1944. Body weights and organ measurements in relation to age and season in ring-necked pheasants. Anat. Rec., 89:175–194.

Kirschbaum, A., and Ringoen, A. R.
1936. Seasonal sexual activity and its experimental modification in the male sparrow, *Passer domesticus* Linnaeus. Anat. Rec., 64:453–473.

Meyer, R. K., Kabat, C., and Buss, I. O.
1947. Early involutionary changes in the post-ovulatory follicles of the ring-necked pheasant. Jour. Wildl. Manag., 11:43–49.

Ramsey, A. O.
1956. Seasonal patterns in the epigamic displays of some surface-feeding ducks. Wilson Bull., 68:275–281.

Seligmann, C. G., and Shattock, S. G.
1914. Observations made to ascertain whether any relation subsists between the seasonal assumption of the "eclipse" plumage in the mallard (*Anas boscas*) and the functions of the testicle. Proc. Zool. Soc. London, pt. 1:23–43.

Southwick, C.
1953. A system of age classification for field studies of waterfowl broods. Jour. Wildl. Manag., 17:1–8.

Sowls, L. K.
1955. Prairie ducks, a study of their behavior, ecology and management (Stackpole Co., Harrisburg, Pa.).

Wolfson, A.
1942. Regulation of spring migration in juncos. Condor, 44:237–263.

Wright, P. L., and Wright, M. H.
1944. The reproductive cycle of the male red-winged blackbird. Condor, 46:46–59.

Department of Zoology, Washington State University, Pullman, Washington, February 18, 1961.