THE REPRODUCTIVE CYCLE OF RING-NECKED PHEASANTS IN MONTANA

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INTRODUCTION

ALTHOUGH the Ring-necked Pheasant, *Phasianus colchicus torquatus*, has been the object of innumerable studies related to its management, comparatively few of these investigations have been concerned with reproductive activities and only two (appearing after the inception of this study) have dealt with the anatomical development of the gonads. The primary objectives of our study were (1) to investigate the gonadal cycle of both sexes in wild birds, and (2) to correlate anatomical data with data derived from field observations on breeding behavior during the same season birds were collected for autopsy. However, the timely appearance of the two studies made on pen-reared birds provided the framework for another major objective, (3) to compare the gonadal cycle of wild birds with that of pen-reared birds. A secondary objective, highly significant from the viewpoint of management, was to secure evidence substantiating or refuting the assumption that pheasants rear a second brood during a single breeding season.

REVIEW OF PREVIOUS STUDIES

Recently, Kirkpatrick (1944a), working over a one-year period in Indiana, performed a series of autopsies on 177 pen-reared Ring-necked Pheasants. He noted that increases in testicular weight began as early as February 16, when the males were 271 days of age. At this time motile sperm was found in the testes, epididymides, and vasa deferentia. Histological observations showed precocious spermatogenesis as early as August and September when the birds were 94 to 109 days of age. The testes attained maximum weight on April 20 at 334 days of age and thereafter followed the usual cycle for adults. In a later paper, Kirkpatrick and Andrews (1944) reported upon a histological examination of the testes of 72 birds of pen-reared stock. Four phases of testicular growth were described. During phase 1 (from time of hatching until the eighty-first day, August 7) the testes underwent a gradual increase in weight; only spermatogonia and a few primary spermatocytes were present. Phase 2, which began on the eighty-first and terminated on the one hundred forty-fourth day (October 15), was characterized by a rapid increase in weight; three of the 18 testes sectioned during this period contained spermatozoa. A period of involution and decreased gonadal weight during which

the seminiferous tubules contained only spermatogonia and a few primary spermatocytes accompanied the third phase, which extended from the one hundred forty-fourth to the two hundred fifty-sixth day (February 10). During the fourth phase, which extended from the two hundred fifty-sixth day to the end of the year (May 18), the testes attained mature size and full spermatogenesis.

Wight (McAtee, 1945) recognized seven phases in the sexual cycle of Ring-necked Pheasants in Michigan. These phases were erected mainly on observational data on the behavior of the birds through an annual cycle. The longest period, "interphase" from late summer until late January or early February, was characterized by solitary cocks whose testes were small and non-functional. Cocks sought hens during the "premating phase" which started as early as February 10; during this period the testes were undergoing rapid recrudescence. The "mating phase" signified by mating [formation of harems?], copulation, and establishment of territories, began about February 27 and merged into the "laying phase" as early as April 12. After this time nests were constructed, eggs were laid, and copulation continued. Copulation terminated at the onset of the "incubating phase," and males no longer associated with hens. The "brooding phase," during which the juveniles were attended by hens and not infrequently by cocks, began as early as April 23 in some years, but most often was initiated in early May. In late summer, "postnuptial phase," the cocks began to molt, testes regressed, and the cocks became solitary. Wight (*op. cit.:* 146) further asserts that both sexes ". . . do not become sexually mature at the same time, hence cocks vanquished by an opponent or slow in maturing become available for females maturing at a later date."

In the domestic fowl, Latimer (1924) recognized some similarity between the growth curve of testes from developing White Leghorn cockerels and the four-phase growth curve characteristic for mammalian testes. He observed (1) a period of slow growth up to 50 days of age; followed by (2) an increase in rate of growth from 50 to 80 days; then (3) a period of rapid or pubertal growth up to 210 days; and (4) a terminal plateau or period following sexual maturity. Hogue and Schnetzler (1937) reported that although wide individual discrepancies occurred, Barred Plymouth Rock males reached sexual maturity as early as 16 weeks of age; however, in pen matings a satisfactory level of fertility was not observed sooner than 26 weeks. During the first eight weeks of life the seminiferous tubules contained chiefly spermatogonia. Testis weight approximately doubled between the eighth and twelfth weeks and primary and secondary spermatocytes were observed.

A testis weight comparable to that of mature males was attained at 18 weeks of age, at which time fully-formed spermatozoa were present. Parker *et al* (1942) found that the development of the testes of White Leghorn and New Hampshire cockerels closely paralleled that found for Barred Plymouth Rock males except for the precocity shown by the latter breed. Mature testis size in White Leghorn and New Hampshire cockerels was attained at 24 and 30 weeks, respectively, but spermatozoa were present in some during the twelfth week. Fertility tests showed that no cockerels which developed spermatozoa at 12 weeks of age were successful in fertilizing hens, but by the twenty-fourth week fertility was general for both breeds.

Kirkpatrick (1944a) reported that his pen-reared pheasants began to lay on April 8, which is approximately two weeks earlier than the earliest date recorded for wild birds by Grinnell *et al* (1918) near San Bernardino, California. Nests have been reported as late as August (Bent, 1932; Grinnell *et al, op. cit.;* and McAtee, 1945). The latest recorded successful hatching date is September 24 (McAtee, 1945: 143). The clutch is incubated from 22 to 26 days.

The question of a second successful brood in one breeding season has been discussed by several investigators. Some confusion has existed because several workers have failed to distinguish clearly between a second successful brood and the phenomenon of renesting following the destruction or desertion of the initial nest. Grinnell (1918: 575) states: "In Oregon it is said that three broods are reared in a season." Beebe (1922: 123) says that the ring-neck in its native Asiatic range sometimes breeds twice, but he makes no similar assertion for the other ancestral line of our American hybrid, *Phasianus colchicus*. Leffingwell (1928: 13) states: ". . . I believe that two broods are often raised as I have found nests as late as August 10th." Wight (1930: 224) says, "Early nesting pheasants usually again build nests and rear a brood," but Leopold (*cf.* McAtee) believes that he refers to renesting, not a second brood, since Wight observed that the cock starts to molt and becomes solitary before the first brood leaves the hen. Attempts at renesting by Michigan pheasants were noted as late as September. Leffingwell (*op. cit.*: 19) states that the cock often leads the brood when the brood is six or seven weeks old which suggested to him that the females were either setting or raising another brood. Leopold (1937: 100) is extremely doubtful that pheasants habitually rear a second brood and believes that second broods are not sufficiently common to exert an effect upon the breeding potential of the species. He believes that the relatively small birds often found in the fall are from late renestings.

Behavior normally associated with the breeding season has been noted at other seasons in several species of gallinaceous birds. Juvenile male Ring-necked Pheasants were observed to crow and to engage in frequent sham battles during August and September (Leffingwell, 1928). Forbush (1927) reported that Ruffed Grouse (*Bonasa umbellus*) copulated in autumn, while Allen (1934) states that this species is known to drum at all seasons. In Wisconsin the Prairie Chicken (*Tympanuchus cupido americanus*) has been observed to boom occasionally in mid-October (Hamerstrom, 1939), and Scott (1942) reported that a few Sage Hens (*Centrocercus urophasianus*) in Wyoming strut sporadically during warm spells in the winter months. Kirkpatrick and Andrews (1944) suggest that gonadal activity outside the usual breeding season may be responsible for the behavior since both Ring-necked Pheasants and domestic fowls show a temporary acceleration in testicular development at approximately 12 weeks of age.

ACKNOWLEDGMENTS

We are deeply grateful to William Bergeson, Senior Wildlife Technician, and Ruth Bergeson, Wildlife Technician, Division of Wildlife Restoration, Montana State Fish and Game Department, for carrying out most of the field duties concerned with this study. We are also indebted to the State of Montana Fish and Game Commission, and to Robert F. Cooney, Director of the Division of Wildlife Restoration, whose understanding of the need for fundamental research in the field of game management made this investigation possible. This study is a portion of Pittman-Robertson project 1-R, 1943.

MATERIALS AND METHODS

Field observations and collections were made in the irrigated valleys of the Yellowstone and Big Horn rivers in the counties of the same names in the vicinity of Billings and Hardin, Montana. Two and often three investigators were in the field during the year beginning in May, 1943, and ending in May, 1944. Early morning roadside censuses which were made at frequent intervals throughout the year enabled the observers to gather data from thousands of pheasants. Several pheasants were collected each week by shooting; by the end of the year 528 birds (319 males and 209 females, juveniles and adults) had been autopsied. Each bird was weighed and the depth of the bursa was measured at autopsy. A glass rod 2 mm. in diameter and scaled in millimeters was used for measuring the depth of the bursa of Fabricius. The vent was opened and the tip of the scale inserted and gently pushed inward with a rotary motion to cause it to be

lubricated from the inner surface of the bursa. This technique is similar to that described by Kirkpatrick (1944b). When the tip reached the blind end of the bursa the scale was released to enable the tissues to resume their normal position. Readings to the nearest millimeter were taken where the edge of the bursa crossed the scale.

Dissections were made, the testes were removed and preserved in a 10 per cent solution of formalin, and the ovarian development was recorded as described on page 539. Later the testes were weighed, the smaller ones on a milligram torsion balance and the larger ones on a chainomatic analytical balance. Each testis was removed from the preservative and gently touched upon a blotter until no more fluid drained from the surface. To check the accuracy of the method, one testis was weighed, resubmersed, and again weighed, in 25 successive trials. The mean weight was 1.349 grams, the standard deviation was 0.0039 grams, and the mean deviation was 0.00328 grams. Since the mean deviation was approximately four-fifths of the standard deviation, a relationship which obtains with distributions near symmetry, our method of weighing was deemed sufficiently accurate.

The largest juvenile and adult testes obtained during each weekly period were selected for sectioning. These were sectioned at 10 microns and stained in iron hematoxylin. After examining and plotting the stages of spermatogenesis found in this first group of testes, a second group was selected from those testes taken at critical times during the annual cycle, *i. e.*, the period of onset of complete spermatogenesis in the spring, the period of involution during the summer, and the period of increased gonadal activity in the fall. A total of 96 testes was sectioned and studied histologically.

Juvenile and adult birds could be distinguished during the summer, fall, and early winter by the depth of the bursa. In all pheasants more than one year of age, the bursa had either disappeared or was less than 11 mm. in depth, while all birds hatched during the spring and summer had a bursa at least 11 mm. in depth until the following January. Thus our findings on bursal depths of wild birds, except for a few minor discrepancies, coincide well with those set forth by Linduska (1943) and Kirkpatrick (1944b) for pen-reared birds.

Our data are usually presented separately for birds without a bursa, birds with a bursa less than 11 mm. in depth, and birds with a bursa 11 mm. or more in depth. The age-weight charts for juvenile pheasants given by Leopold (1937) and by Kirkpatrick (1944a) were utilized to ascertain the approximate age of some of the immature birds reported upon in this study. Despite the inaccuracies involved in using such charts formulated from data secured from pen-reared birds, the error is probably less than if the ages were merely estimated.

RESULTS OF THIS STUDY

The influence of age and season on testis weight for birds with a bursa at least 11 mm. in depth is summarized in Table 1. In these juvenile birds three growth phases were evident in the period from July to March. The first phase was characterized by a rather rapid increase in testis weight from July to September, with the mean testis weight doubling during each month. During this period the standard errors of the monthly means were very low and the coefficients of variation were large. The large coefficients of variation indicate the great individual variation in development which accompanies the rapid change in weight. The second phase extended from October through January during which time the monthly means of testis

TABLE 1

STATISTICAL SUMMARY OF THE GROWTH RATE OF RING-NECKED PHEASANT TESTES IN BIRDS WITH A BURSA AT LEAST 11 MILLIMETERS IN DEPTH

Month	*Number of testes examined*	*Range in weight (grams)*	*Mean weight (grams)*	*Standard error of the mean*	*Standard deviation*	*Coefficient of variation*	*Standard error of the coefficient of variation*
July	4	0.015–0.033	0.023	±0.004	±0.009	37.4	±13.21
August	26	0.010–0.104	0.041	±0.005	±0.026	63.7	± 8.84
September	26	0.024–0.267	0.088	±0.009	±0.048	54.0	± 7.48
October	42	0.038–0.125	0.082	±0.003	±0.019	23.3	± 2.51
November	20	0.045–0.098	0.066	±0.004	±0.018	27.9	± 4.41
December	8	0.046–0.101	0.065	±0.007	±0.019	29.4	± 7.35
January	17	0.045–0.130	0.079	±0.059	±0.025	31.0	± 5.31
February	11	0.026–0.295	0.146	±0.026	±0.087	59.6	±12.68
March	9	0.210–3.840	1.530	±0.419	±1.257	82.1	±19.33

weights were somewhat less than in the preceding period, and little change in weight occurred. In all young birds examined, the standard errors of the means continued low until January, but the coefficients of variation were smaller than in the initial growth phase, indicating less individual variation during this period of practically constant testis weight. Mean testis weight showed an upward trend in late January and was doubled in February when the third growth phase was initiated. An extremely rapid testicular development occurred in late February and early March, at which time the gonad reached the apex of its development for birds still distinguishable as immatures. Correspondingly high standard errors of the means and large coefficients of variation occurred in February and March,—demonstrating much variation between individuals in this time of greatest increase in testicular weight.

The influence of age and season on testis weights in birds with a

bursa either less than 11 mm. in depth or without a bursa is summarized in Table 2. Three growth phases were apparent during the annual cycle. The first phase began in mid-May, at which time mean testicular weights reached a maximum, and terminated about September 1, signifying the approximate end of involution. The standard errors of the mean gonadal weights were greater in this period than at any other time of the year, but within the period they were comparatively low from mid-May to June, increased during July, and were rather large in August. A comparable trend for the coefficients of variation was apparent, with the highest value in August. The relatively high standard error and coefficient of variation in August

TABLE 2

STATISTICAL SUMMARY OF THE GROWTH RATE OF RING-NECKED PHEASANT TESTES IN BIRDS WITH A BURSA LESS THAN 11 MILLIMETERS IN DEPTH OR WITHOUT A BURSA

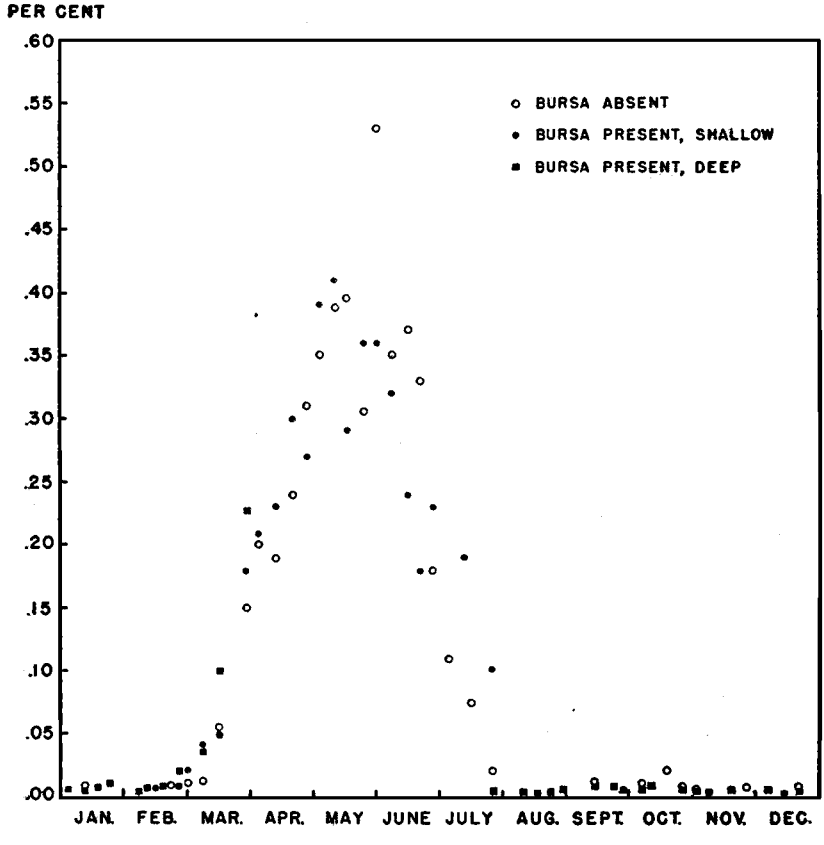
Month	*Number of testes examined*	*Range in weight (grams)*	*Mean weight (grams)*	*Standard error of the mean*	*Standard deviation*	*Coefficient of variation*	*Standard error of the coefficient of variation*
January	3	0.054–0.172	0.097	±0.038	±0.065	66.8	±27.25
February	23	0.056–0.420	0.176	±0.023	±0.108	61.6	± 9.09
March	47	0.193–3.746	1.334	±0.137	±0.943	70.6	± 7.28
April	45	1.539–5.449	3.259	±0.136	±0.911	27.9	± 2.94
May	60	2.314–7.556	4.564	±0.162	±1.253	27.5	± 2.51
June	45	1.711–8.093	3.587	±0.199	±1.338	37.3	± 3.93
July	16	0.726–2.914	1.633	±0.170	±0.681	41.7	± 7.37
August	8	0.183–1.562	0.788	±0.192	±0.543	68.9	±17.20
September	2	0.182–0.184	0.183	——	——	——	——
October	14	0.070–0.173	0.117	±0.010	±0.036	30.9	± 5.84
November	4	0.076–0.098	0.089	±0.005	±0.010	10.5	± 3.71
December	2	0.100–0.117	0.109	——	——	——	——

indicate a period of rapid change, and further show that involution of the testis does not occur simultaneously in all birds. The second growth phase which began early in September extended to mid-February. The minimal testis weights showed little change from October to February, and the interval was characterized by little or no activity in the regressed gonads. However, that recrudescence starts in February is demonstrated by the much higher maximal testis weight in this month. The standard errors of the mean testis weights are comparatively low except in January when the error was unusually high, perhaps due to statistical errors resulting from the small sample examined. By October most testes have regressed to approximately the same level and the coefficient of variation diminishes accordingly. During the latter part of this phase testicular activity started slowly and apparently differentially among the birds because

the coefficient of variation increased several-fold over the early winter months. The rapid recrudescence of the testes in mid-February marked the beginning of the third phase which terminated when the testes attained their maximum weight in mid-May. Considerable individual variability in development was apparent during February and March as shown by the fact that the standard errors of mean testicular weights were comparatively high as were the coefficients of variation which reached their maximum value in March. However, there does not seem to be as much individual variation in recrudescence as in regression, judging from the values of the standard errors and the coefficients of variation. Variation in testicular weights was greatly reduced during April and May, and we may assume that most birds have reached and are maintaining a maximal testis weight.

To minimize the extensive variation in testis weights for better illustration of testis development in relation to age and season (Text-figure 1), the testis weight was expressed in percentage of body weight, and mean weekly ratios were plotted for: (1) birds without a bursa; (2) birds with a bursa less than 11 mm. deep (shallow); and, (3) birds with a bursa at least 11 mm. in depth (deep). Because of rapid increases in testis weight, the ratios of testis weight to body weight first changed perceptibly for both yearlings and adults during the latter part of February. No differences between age classes were noted in the time of increase or in the amount of increase. Maximum testis weights were attained by mid-May. Involution was initiated in late May, was greatly accelerated in June, and became complete by the end of August. Birds of the year showed a significant increase in testis weight in September and October, after which time full regression ensued. The gonads of all males remained small from November until early February.

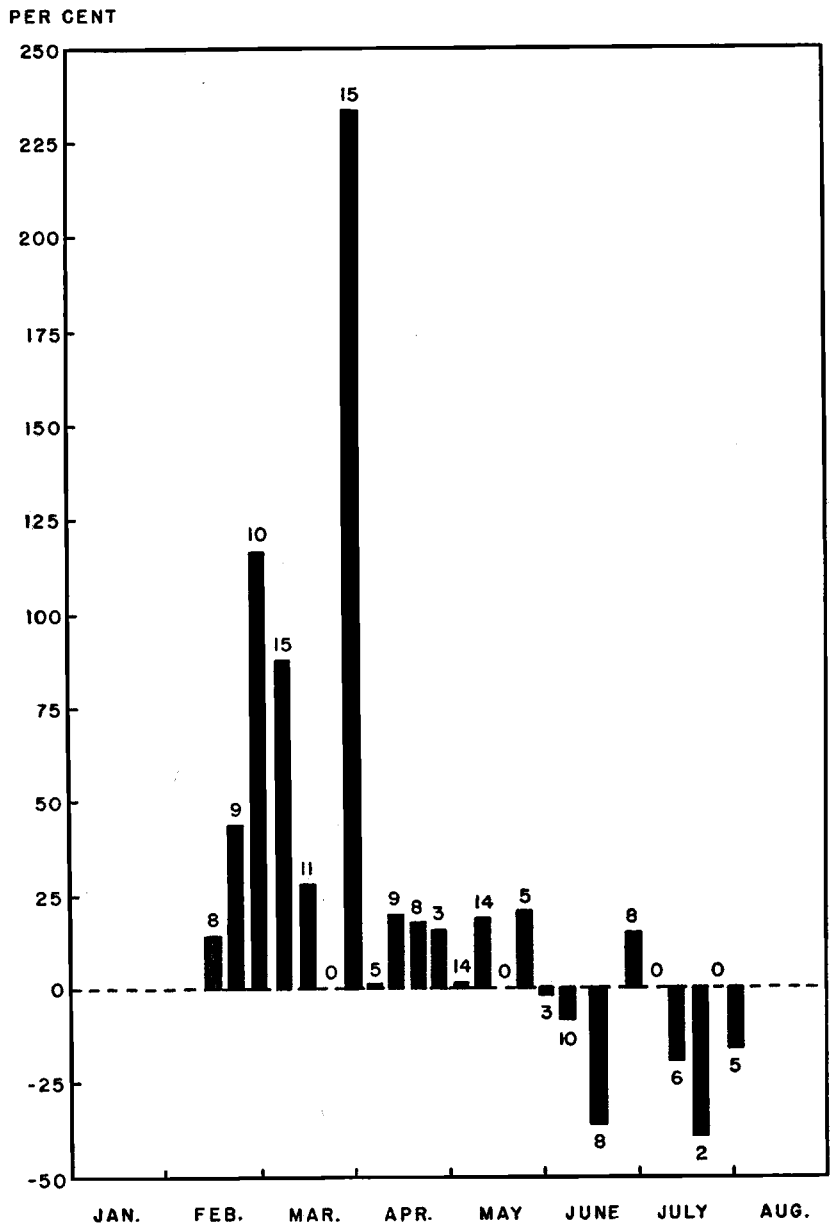
The rate of recrudescence in the spring for testes of all age classes was analyzed critically by ascertaining mean weekly weights and computing the percentage of increase in weight over the mean weight for the previous week (Text-figure 2). Because no significant change in weight occurred through January and the first week in February, the mean weight of testes examined during this period was selected as the initial weight. Rapid increases in weight occurred for the first three weeks or to about March 1 after which the rate of growth diminished until mid-March. The greatest weight increment occurred in the two-week period between mid-March and April 1 in which time the testes more than tripled their weight. After this date the rate of increment was much less but remained steady until the latter part of May. Reduction in weight began in late May and early June and



TEXT-FIGURE 1.—Testes weights of Ring-necked Pheasants in relation to season in Montana. Weights are expressed in percentage of body weight.

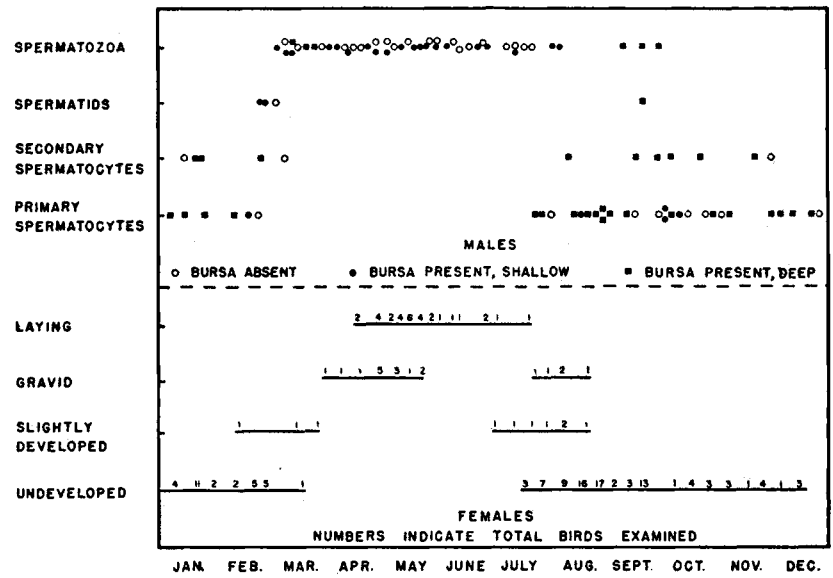
continued through July at a slow rate except for a brief period in late June and early July when, inexplicably, a slight increment in weight occurred.

The data derived from the histological study of spermatogenesis and the gross anatomical survey of oogenesis are presented schematically for comparison in Text-figure 3. Spermatogenesis is closely associated with the three growth phases mentioned for young birds (Table 1) and with the three growth phases indicated for older birds (Table 2). Spermatogonia and primary spermatocytes were present during all months of the year. Spermatogenesis was initiated in January when birds of all age classes developed secondary spermatocytes. By the latter part of February spermatids were present in birds



TEXT-FIGURE 2.—The average weekly rate of change in weight in testes of breeding Ring-necked Pheasants in Montana. The bars indicate the change in weight expressed as percentage of the average weight for the previous week. The number of testes weighed during each period is inserted at the end of the bar.

of all age classes and mature spermatozoa appeared in all testes taken after March 8; the first spermatozoa were noted on March 3. The smallest testis to come into complete spermatogenesis in the spring weighed 0.781 grams. The bird (number 449) weighed 1368 grams and had a bursa 14 mm. in depth which indicated that it was a bird of the year. The heaviest testis examined weighed 8.093 grams. It was taken from a bird weighing 1462 grams collected on June 1; no bursa was present. All adult birds contained mature spermatozoa until



TEXT-FIGURE 3.—A comparison of gametogenesis in Ring-necked Pheasants in Montana with relation to season. Only the most advanced stage of each gonad is indicated. The numbers above the lines indicate the number of specimens examined. For an explanation of the developmental stages employed for females refer to p. 539.

August 1 and one yearling had spermatozoa on August 6. Regression was abrupt during early August, and the testes of all year-old and adult birds remained completely regressed until January except for one whose seminiferous tubules contained a few secondary spermatocytes on December 1.

All birds of the year had primary spermatocytes after July 22, and one, approximately 80 days of age, contained secondary spermatocytes on August 11. All juvenile birds examined from September 15 to October 7 contained testes in an advanced stage of spermatogenesis and three contained mature spermatozoa during September. Pertinent descriptive data for these three birds are set forth in Table 3.

TABLE 3

DESCRIPTIVE DATA FOR THREE JUVENILE MALE RING-NECKED PHEASANTS WHICH UNDERWENT COMPLETE SPERMATOGENESIS IN SEPTEMBER

Collection number	*Weight of bird (grams)*	*Approximate age (days)*	*Approximate date of hatching*	*Testis weight (grams)*	*Depth of bursa (millimeters)*
259	1456	?[1]	?	0.125	22
291	1275	135	May 20	0.267	28
298	807	80	July 12	0.049	24

[1] Determination of ages from age-weight curves is impractical when young birds reach the approximate weight of adults.

Ovarian development was grossly classified into four categories: (1) "undeveloped," no Graafian follicles visible; (2) "slightly developed," follicles less than 5 mm. in diameter; (3) "gravid," follicles at least 5 mm. in diameter, and small eggs sometimes present in the oviducts; (4) "laying," eggs in the oviducts large, generally with a shell. Graafian follicles made their appearance in mid-February and small eggs were present in the oviduct by the end of March. Laying females were collected from mid-April to mid-July after which time no large eggs were noted in the oviducts although large Graafian follicles were present until late August. No evidence of oogenesis was found

TABLE 4

SUMMARY OF THE FORMATION AND DISSOLUTION OF RING-NECKED PHEASANT HAREMS IN MONTANA

Period	*Number of observations*	*Total number of birds observed*	*Birds in harems (percentage of total)*	*Total number of harems observed*	*Incidence of harems in percentage of total observations*
Mar. 16–23	129	888	0.0	0	0.0
Mar. 24–31	142	677	5.8	5	3.5
Apr. 1–7	33	112	15.2	2	6.1
Apr. 8–15	32	99	29.2	7	21.8
Apr. 16–23	28	143	55.2	18	64.2
Apr. 24–30	57	123	66.7	25	43.8
May 1–7	123	297	74.4	63	51.2
May 8–15	126	349	79.1	77	61.1
May 16–31	10	21	80.9	6	60.0
June 1–7	276	558	67.2	118	42.8
June 8–15	177	385	70.9	88	50.0
June 16–23	161	315	58.7	66	41.0
June 24–30	150	288	63.1	63	42.0
July 1–7	125	261	39.8	39	31.2
July 8–15	124	303	22.4	27	21.7
July 16–23	89	264	15.5	15	16.8
July 24–31	86	263	4.9	7	8.1
Aug. 1–7	110	416	2.9	5	4.5
Aug. 8–15	89	403	0.5	1	1.1
Aug. 16–23	80	436	0.0	0	0.0

in any juvenal females. All ovaries remained quiescent from late August to mid-February.

Behavior associated with gonadal development was analyzed through field observations. A summary of the formation and dissolution of harems of Ring-necked Pheasants during the study period is presented in Table 4. More harems were found in May than in any other month. At this time about 80 per cent of all the birds were associated in harems and three-fifths of all observations were those of birds in harems. By mid-August the cocks were either solitary or attending broods, and most of the hens were attending broods.

The first nest observed (April 15) contained an incomplete clutch

TABLE 5

SUMMARY OF FIELD OBSERVATIONS ON BROODS AND YOUNG OF RING-NECKED PHEASANTS IN MONTANA

Period	*Number of observations*	*Total number of birds observed*	*Number of broods observed*	*Total number of young observed*	*Average brood size*	*Young in population (percentage of total)*
June 1–15	11	682	1	5	5.0	0.7
June 16–30	19	550	6	15	2.5	2.7
July 1–15	19	491	23	119	5.2	24.2
July 16–31	17	459	57	260	4.6	56.6
Aug. 1–15	15	832	116	630	5.4	75.7
Aug. 16–31	17	1014	150	844	5.6	83.2
Sept. 1–15	8	402	67	279	4.2	69.4
Sept. 16–30	8	635	72	370	5.1	58.2
Oct. 1–15	12	1112	20	124	6.2	11.1
Oct. 16–30	13	1237	1	1	1.0	0.0
Nov. 1–15	6	181	0	0	0.0	0.0

of eggs. The last nest still being covered was recorded on July 27. Further evidence on late nesting was obtained indirectly by computing from age-weight curves the approximate hatching dates of young collected during the late fall and early winter. On December 16 an immature female weighing 715 grams and having a bursal depth of 22 mm. was collected. This bird was approximately 95 days of age which would set the hatching date about September 13. Several others are presumed to have hatched during August, judging from similar evidence.

A summary of the observations made on the occurrence of broods is presented in Table 5. The first brood, with young about the size of a Meadowlark, was observed on June 5 which indicates that the hatching date was in late May. Hatching dates computed from weights of collected juveniles also indicated that the earliest hatching occurred in the latter part of May. During August more than three-fourths of

all birds observed were immature. The last observed brood of the year was found on October 22; the young appeared to approximate adult size and were attended by a hen. After this date it was impossible to distinguish individual broods.

Attendance to broods by adult pheasants is analyzed in Table 6. Several trends, to be more fully discussed later, may be observed in this table. From June to October there was a constant decrease in the percentage of broods attended by one or more hens. From July to October there was an increase in the percentage of broods attended by a cock only, and there was also a gradual increase in the percentage of broods with no attendant adults.

TABLE 6

ATTENDANCE TO BROODS BY ADULT RING-NECKED PHEASANTS IN MONTANA

Month	*Number of broods observed*	*Percentage of broods attended by one hen*	*Percentage of broods attended by more than one hen*	*Percentage of broods attended by both cocks and hens*	*Percentage of broods attended by a cock only*	*Percentage of broods unattended*
June	7	86	0.0	0.0	0.0	14
July	80	56	11	13	1	19
August	266	56	4	8	3	29
September	139	34	0.0	9	22	35
October	21	43	0.0	9	24	24

DISCUSSION

The anatomical data presented in this study on wild male Ring-necked Pheasants are closely comparable to the findings of Kirkpatrick (1944a) and Kirkpatrick and Andrews (1944) for pen-reared birds. Since the present paper deals with a wild population, it was obligatory that immature birds be dissociated from adults. Consequently, only data for immature birds can be used for comparison with previous studies; heretofore, no investigation of sexual rhythms in adults has been undertaken.

Kirkpatrick and Andrews (*op. cit.*) find two phases of testicular growth from June to October, the first of which they state is characterized by a very gradual increase in testis weight, terminating about the first week in August. The second phase is termed one of rapid increase in testis weight. Actually, their figures show a weight increment of almost 6000 per cent and 225 per cent for the two phases, respectively. It would seem that the terms "very gradual increase" and "rapid increase" should be exchanged. Our data show the growth to be rather rapid and constant from July to late September; consequently, our first growth phase coincides with the first two growth

phases of the above workers. Our phases 2 and 3 correspond very closely to their phases 3 and 4. Three growth phases are adequate to describe the gonadal activity of adult male birds. Only the third phase coincides in all age classes, and no off-season development such as is characteristic of juvenile birds in September occurs in the older pheasants. Since individual variation in testicular development is greatest from January through March, and since this variation diminishes greatly during the mid-breeding season months from April to July, it is apparent that the rapid development of the testes in early spring is not simultaneous for all males, but that all birds reach approximately the same level of testis weight in April and early May. Similarly, the increasing variation in mean testis weights from June through August indicates that a differential involution occurs.

Spermatogenesis in our wild birds coincided almost exactly with that described by Kirkpatrick and Andrews for pen-reared stock. Moreover, considerable similarity in time was noted between spermatogenesis in juvenile pheasants and in juvenile domestic fowls. In both species increased gonadal activity begins between the eighth and twelfth weeks with complete spermatogenesis occurring in some at the end of the twelfth week. Some individuals of both pen-reared and wild pheasants attained complete spermatogenesis at about 80 days of age. However, domestic fowls which developed spermatozoa at 12 weeks of age were shown to be infertile at that time, and it seems likely that these precocious pheasants are similarly infertile.

Kirkpatrick and Andrews suggest that a like period of off-season gonadal activity may occur in some native gallinaceous birds. This may explain the courtship behavior found at this time, but which is normally associated with the breeding season. The data secured from both pen-reared and wild pheasants provide good presumptive evidence for this hypothesis, but our data show that such off-seasonal gonadal activity is characteristic only for male birds of the year and does not occur in older birds. This would indicate that perhaps only young males participate in these extra-seasonal patterns of behavior.

As in pen-reared pheasants (Kirkpatrick, 1944b; Kirkpatrick and Andrews, 1944) and doves (Riddle, 1928), the bursae of our juvenile wild pheasants attained maximal depths at the period of spermatogenic activity in September, and involution of both the testis and the bursa began immediately afterward. The above workers also noted that the thymus behaved similarly to the bursa. Our data provide further circumstantial evidence that testicular activity of young pheasants is physiologically associated with the subsequent involution

of the bursa, and that the bursa may have an endocrine function, particularly in view of the experimental evidence secured by Kirkpatrick and Andrews who produced highly significant decreases in bursal depths in sexually immature pheasants by injecting testosterone proprionate into normal and castrated males, and stilbestrol into normal females.

Nesting in Montana begins in April, the month in which nesting is reportedly undertaken in other sections of the United States. The nesting season in Montana extends into mid-September, which closely approaches the time of the last successful nesting recorded in the literature.

Male birds preceded females by approximately one month in attaining complete gametogenesis in the spring. Since complete spermatogenesis was achieved in all males within a period of two weeks in late February and early March, and since the ovaries in all females reached laying condition in a period of two weeks in late March and April, there is little factual basis for the statement of Wight that cocks vanquished by an opponent or cocks slow in maturing become available for those females which are slower to mature. The period comparable to the "premating phase" of Wight was devoted by the males to seeking hens and establishing territories. By late March a few harems had been formed, and copulation began. Within a month over one-half of the birds were segregated into harems; at this time all birds were capable of reproduction. By June 1 the number of harems began to diminish and broods appeared. The ovaries of some hens were inactive by mid-July, and in most hens this stage was reached by August 1. Gonadal involution in males was likewise complete in August. They became either solitary or attended broods after this time. The maximum number of broods was reached by mid-August.

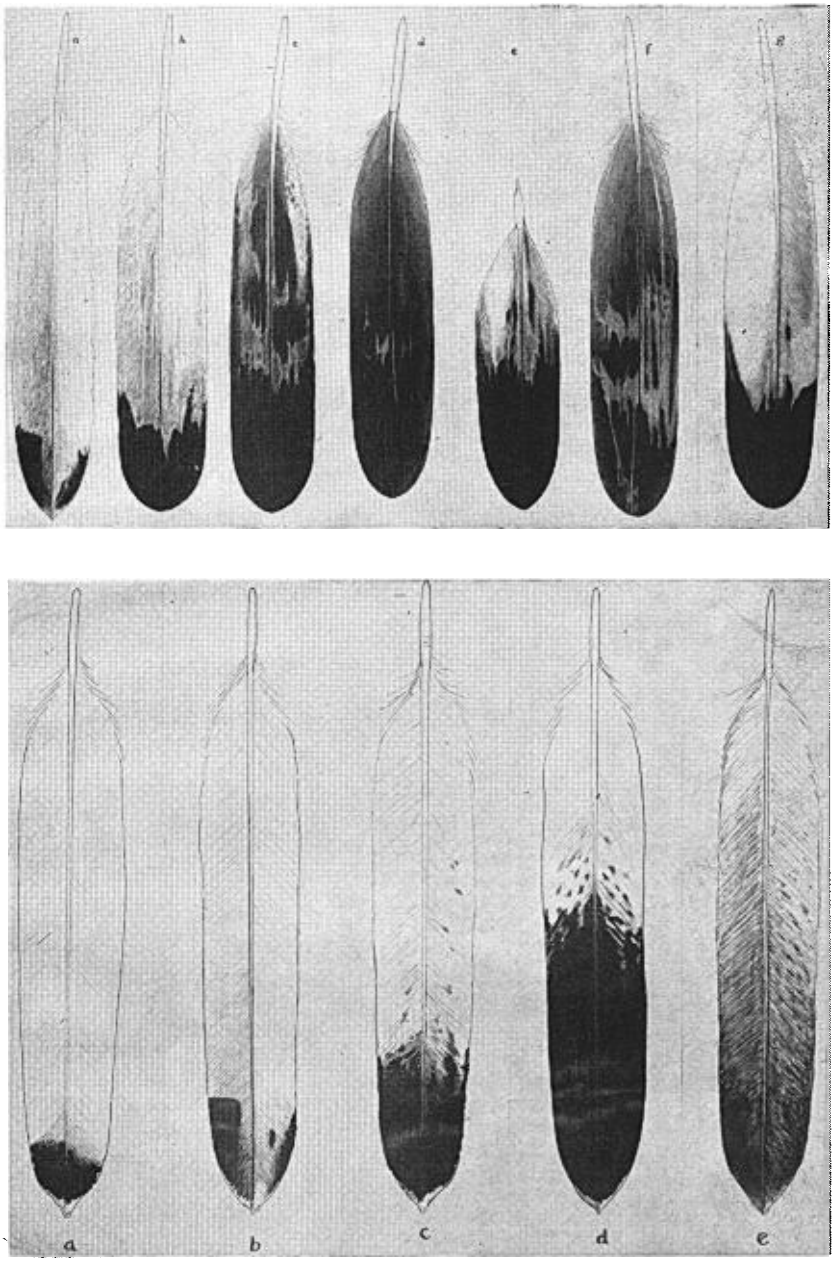
Although we have no direct observational data to demonstrate whether or not Ring-necked Pheasants in Montana raise more than one brood per season, sufficient facts are at hand to compute the possibility and the probability of such an occurrence. The days required for rearing a brood successfully, as ascertained by this study are:

Days	*Item*	*Calculation*
18	Laying	12 eggs at 1½ days per egg
2	Interval	
24	Incubation	22 to 26 days
80	Dependency of young	Period until half-grown
Total 124		

A hen starting her first clutch on April 15, the earliest date on which eggs were found and the theoretical date of first possible laying (*see* Text-figure 3), could therefore not rear that brood and be ready to start a second before 124 days had elapsed, or on August 16. A new nest started then would hatch about September 28 and the young would not be independent until December 16.

Our data provide considerable circumstantial evidence opposing the possibility of a second brood as outlined above. Since cocks with mature spermatozoa were not found in the population after the first week in August, impregnation of the female would necessarily have to occur on or before this time. No laying hens were found among birds autopsied after late July, but a small proportion had gravid ovaries through mid-August. Hens starting to lay a clutch on August 16 would have had to retain viable spermatozoa for a period of about 10 days. Whether or not such retention in pheasants is possible is unknown, but female domestic fowl retain spermatozoa which effect a high degree of fertility for 10 days to two weeks. A rapid decrement in fertility ensues two weeks after impregnation, with a small proportion of eggs fertilized for as long as one month. Although a second brood is possible under such circumstances, it is highly improbable that most hens would begin the first nest on April 15, which is the earliest possible date, or that they would follow the rigid schedule of time required for two broods. It has already been pointed out that the last nest observed was on July 27 but that by computing the hatching date from the weight of an immature bird, the last hatching could have occurred about September 13 (two weeks before a second brood could have been hatched), which probably means that this is an instance of renesting. Thus, no field or laboratory evidence we have supports actively the hypothesis of a second brood.

However, the discussion above is predicated on the assumption that the hen attends her brood for an average of 80 days, at which time the chicks are about half-grown. There remains the possibility that some hens desert the young short of 80 days while others may remain with the brood until the young approximate adult size. The hen's activity in this regard is of great importance in any consideration of second broods. The data presented in Table 6 indicate that in July and early August about one-fourth of the broods were unattended by hens, and in addition about one-tenth of the hens were traveling with a brood also attended by a cock. It is evident that one-fourth of the hens were unaccounted for during July and early August. It is conceivable, therefore, that as Leffingwell (1928) suggested, some of these missing hens and some of those associated with cocks in dual attendance on



GOLDEN EAGLE: (*Upper*) THE THREE CLASSES OF PATTERN ON RECTRICES AS PRODUCED BY SMOKY: a, b, c, d ARE FEATHERS PRODUCED BY LEFT-CENTER PAPILLA; e, f BY RIGHT-CENTER PAPILLA; g IS A SUBADULT FEATHER NEXT TO RIGHT CENTER (*see* TEXT-FIG. 6). (*Lower*) VARIATION AMONG JUVENAL RECTRICES (CENTRAL TAIL FEATHERS, LEFT SIDE).

broods might breed and rear another brood. It is interesting to note in this same table that attendance to broods by hens declines as the breeding season progresses while the attendance to broods by cocks increases. Thus there is a distinct possibility that second broods may be produced by that small group of hens which desert their broods in July and early August. However, the precipitous decline in gonadal activity in both sexes by the end of July, the sharp reduction in number of broods observed in early October, the virtual absence of broods after late October, and the disappearance of most of the harems after mid-July suggest that second broods are certainly infrequently produced if at all. In any event, it is extremely doubtful if two broods occur frequently enough in Montana to exert any appreciable effect on the breeding potential of the species. The assertion made by the informant to Grinnell *et al* (1918) that three broods are reared in a season in Oregon seems absurd, and the statement by Beebe (1922) that the Ring-necked Pheasant sometimes breeds twice in its native Asiatic range lacks factual supporting data.

Many, if not most, of the late nests are undoubtedly the result of renesting. Since both males and females are fertile by mid-April, it seems reasonable to expect that most females have completed their nesting by July 1. Nesting attempts after this date were probably made by hens whose initial nests were destroyed or abandoned before hatching.

SUMMARY

1. The present investigation was undertaken to study the gonadal cycle of both sexes of wild Ring-necked Pheasants, to correlate anatomical and histological data with those derived from field observations on breeding behavior, and to compare the gonadal cycles of wild and pen-reared birds. Circumstantial evidence bearing on the possibility of second broods was also sought.

2. Field observations and collections were made from May, 1943, to May, 1944, in the irrigated valleys of the Yellowstone and Big Horn rivers in the vicinity of Billings and Hardin, Montana. A total of 319 cocks and 209 hens, both juvenile and adult, were collected and autopsied throughout the year. Ninety-six testes of juveniles and adults were sectioned and studied histologically. Age classes were selected on the bases of body weight and depth of the bursa of Fabricius.

3. Three growth phases of the testis, closely correlated with spermatogenic activity, were apparent for sexually immature males. The first phase, from hatching until September, was characterized by a

rather rapid increase in testis weight, and by seminiferous tubules containing only spermatogonia and primary spermatocytes until August 11, when secondary spermatocytes appeared. During September, three of the testes of ten juvenile birds contained spermatozoa. The second phase, which extended from October through January, was characterized by slight gonadal involution and general dormancy until spermatogenesis was begun in late January. Extremely rapid testicular development took place at the beginning of the third phase which ran to early March, after which time the birds were no longer distinguishable as immatures and spermatogenesis coincided with that of the adults. Full spermatogenesis was attained by early March.

4. In adult birds, three growth phases of the testis were likewise apparent. The first phase began in mid-May when testis weights reached a maximum and the seminiferous tubules of all testes contained abundant sperm. The phase extended to September 1 when involution was complete; but no sperm was found after August 4. The second phase, which was the interval between September 1 and mid-February, was characterized by little or no activity in the regressed gonads. Spermatogonia and a few primary spermatocytes were present during this quiescent interval, but we found no off-season spermatogenic activity similar to that present in some precocious pheasants and domestic fowl. The rapid recrudescence of the testis in mid-February marked the beginning of the third phase which terminated in mid-May when the testes were at maximal weights. By the second week in March, all cocks were in breeding condition and remained so until about August 4.

5. No differential testicular recrudescence between the various age classes occurred in the spring. Although recrudescence was rapid, the rate was irregular. Rapid weight increments occurred until about March 1 after which the growth rate diminished for two weeks. The greatest increment in weight took place in the last half of March when the testes more than tripled their size. A slower rate of growth ensued until mid-May when involution began. The high rate of recrudescence in early spring was not simultaneous for all males, but all reached sexual maturity within a period of two weeks. A differential involution likewise occurred over a relatively brief period; it showed more variability than did recrudescence.

6. Spermatogenesis in wild birds coincided almost exactly with that described for pen-reared birds, and considerable similarity was noted in the testicular activity of juvenile pheasants and juvenile domestic fowls.

7. Graafian follicles were first observed in mid-February, and eggs were present in the oviducts by late March. Laying females were

first noted in mid-April. No laying females were found after mid-July, but small eggs were present in the oviducts until late August. Juvenile females do not undergo off-season gonadal development as do young males.

8. Harem formation was first noted in late March and reached a peak in May when about 80 per cent of all birds were associated in harems. By June 1, the number of harems began to decrease and broods appeared. A rapid dissolution of harems occurred after July 23, and no harems were present after August 10.

9. The extent and season of nesting in Montana is the same as in other sections of the United States. The first nest (clutch incomplete) was observed on April 15, and the last active nesting was recorded on July 27. By computing approximate hatching dates for juvenile birds collected during late fall and early winter, it was found that the latest time of hatching was probably mid-September.

10. The first brood, composed of small chicks, made its appearance on June 5, indicating that hatching occurred in late May. The frequency of broods attained a peak in late August when 83 per cent of all birds seen were juveniles in broods. No broods could be recognized after October 20.

11. About one-fourth of the broods in July and early August were unattended by hens; most of these broods were unattended by any adult, and the remainder of them were attended by the cock alone. Three-fifths of the broods were accompanied by hens and one-tenth were accompanied by both parents. Attendance of broods by hens declined as the breeding season progressed while the attendance of broods by cocks increased.

12. The probability of hens rearing a second successful brood was found to be remote but possible for those hens which deserted their broods in July and early August. The precipitous decline in gonadal activity for both sexes by the end of July, the sharp reduction in number of broods observed in early October, and the dissolution of harems after mid-July suggested that second broods were indeed rare in Montana and exerted no appreciable effect on the breeding potential of the species.

13. Nesting after July 1 is probably renesting.

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