THE ANNUAL GONAD AND THYROID CYCLES OF THE ENGLISH SPARROW IN SOUTHERN CALIFORNIA

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The annual gonad and thyroid cycles of the English Sparrow (*Passer domesticus*) in southern California were investigated in order to establish their nature in an area of mild winter climate, to provide data for comparison with the annual cycles of this species which have been described from areas subject to lower winter temperatures and greater seasonal change, and to see whether any correlation exists between the gonad and thyroid cycles.

The testis cycle of the English Sparrow has been described from Norman, Oklahoma, from November, 1932, to November, 1933, by Allender (1936*a*, 1936*b*) and from Minneapolis-St. Paul, Minnesota, from October, 1932, to March, 1933, by Kirschbaum and Ringoen (1936).

The thyroid cycle of the English Sparrow has been described from several localities. Although there are differences in the findings reported by certain workers, the general pattern in this and other species is one of thyroid activity prior to molt and during the colder months of the year. It has been demonstrated experimentally that the exposure of English Sparrows to low temperature will induce a high level of thyroid activity (D. S. Miller, 1939). Höhn (1950) has reviewed the more important literature on the avian thyroid.

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MATERIALS AND METHODS

This study is based on the microscopic examination of the testes of 95 male English Sparrows, the thyroids of 91 males and 64 females, and the macroscopic examination of the reproductive tracts of 69 females. These birds were collected from June 3, 1952, to July 15, 1953. Most of them were live-trapped in Pasadena, Los Angeles County, California. All others were caught within six miles of central Pasadena. The testes and thyroids were removed and fixed within a few minutes after each bird was killed. The testes were measured to the nearest 0.5 mm. All birds were skinned and examined for subcutaneous fat deposits and degree of skull ossification. The skins were saved and examined for evidence of molt. The bill color of each male was noted, since Keck (1932) has shown that the bill changes from brown and horn in sexually inactive males to black in sexually active males. The ovary and oviduct of each female were examined, and the presence or absence of a brood patch was noted.

Testes and thyroids were prepared for microscopic examination as follows: after fixation in Bouin's solution and preparation by the dioxane-paraffin method, they were

sectioned at 8μ (a few were sectioned at 10μ) and stained with Harris' hematoxylin and eosin.

In order to indicate the amount of spermatogenic activity showed by the testes examined, the six stages of histologic development outlined for *Passer domesticus* by Bartholomew (1949) were used. These are as follows:

Stage 1. Resting spermatogonia only.
Stage 2. Spermatogonia dividing, but only a few spermatocytes present.
Stage 3. Many spermatocytes present.
Stage 4. Spermatocytes and spermatids.
Stage 5. Spermatids and a few spermatozoa.
Stage 6. Full spermatogenic activity with many spermatozoa.

Center sections of at least one testis from each animal were examined and assigned to one of the foregoing stages.

Thyroid activity was difficult to evaluate because most of the glands examined during this study presented a composite picture, a given center section containing appreciable numbers of follicles which were in active, inactive, and intermediate stages of epithelial development. The same difficulty existed with respect to follicle size. Although the average difference in the size of follicles between an inactive and a highly active gland could be easily perceived (figs. 1 and 2), it was difficult to express this difference quantitatively. The selection of an arbitrary number of follicles to be measured for size would be purely subjective, and in the highly composite thyroids studied here, where even in a very active gland considerable numbers of large follicles exist, the sets of figures derived from such measurements would probably be similar for glands in active, inactive, and intermediate stages of development. It should be further noted that the variability in epithelial development extended even to the follicle level, where within a given follicle, cells of two or three different developmental types often existed side by side (figs. 4, 5).

Since the glands to be studied were of such a heterogeneous nature, it was felt that the state of development of the individual epithelial cells would be the most objective index to use in assaying general thyroid activity. Thus, on the basis of relative cell height, cell configuration, and nuclear configuration, five stages of epithelial development were distinguished, as follows:

Stage 1. Epithelium very flat (0.63–1.43μ); nucleus flat or crescentic, very darkly staining, in contact with cell membrane (fig. 3).
Stage 2. Epithelium flat (2.4–3.3μ); nucleus narrowly oval to oval, and in contact with cell membrane (figs. 3 and 4).
Stage 3. Epithelium moderately flat (3.8–5.7μ); nucleus broadly oval to round and may or may not touch cell membrane (figs. 4 and 5).
Stage 4. Epithelium cuboidal (6.65–8.55μ); nucleus round, in contact with cell membrane (if at all) at base of cell away from lumen (fig. 5).
Stage 5. Epithelium columnar or conical, protruding into lumen (8.55–15.2μ); nucleus round and located at base of cell away from lumen (fig. 6).

Cells in stages 1, early 2, late 3, 4, and 5 were easily distinguished; those in late 2 and early 3 were more difficult to distinguish, and a certain amount of subjectivity entered into the method when such cells were encountered. To reduce this subjectivity to a minimum, all classification of cells into stages was done by one person (the junior author). In actual practice, epithelial heights were not measured; the heights are presented merely to describe more exactly the stages present.

Using the foregoing criteria, the index of thyroid activity was determined for center sections of at least one lobe of all thyroids, as follows:

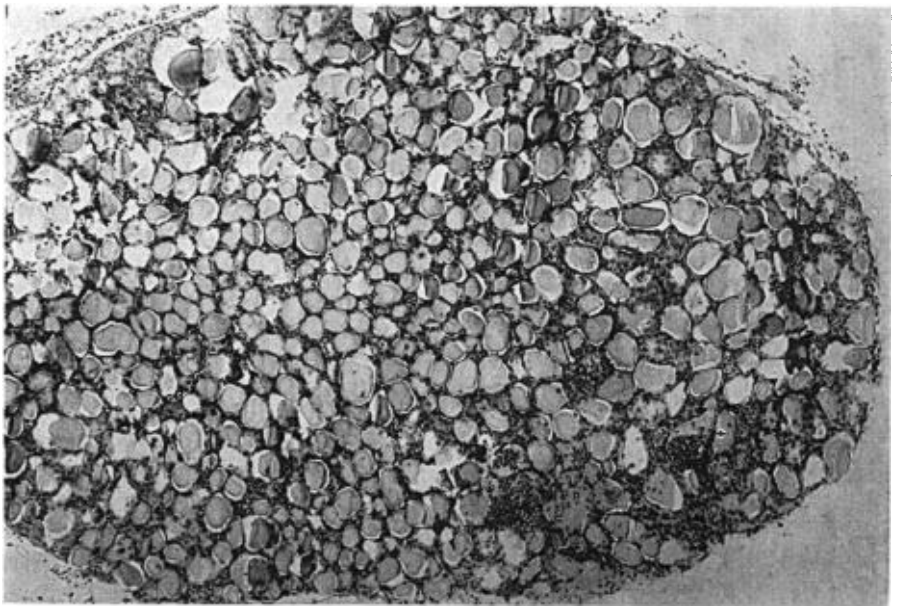

Fig. 1. Cross section of inactive thyroid (index 1.71) from breeding ♂, no. 141, May 2, 1953, × 162.

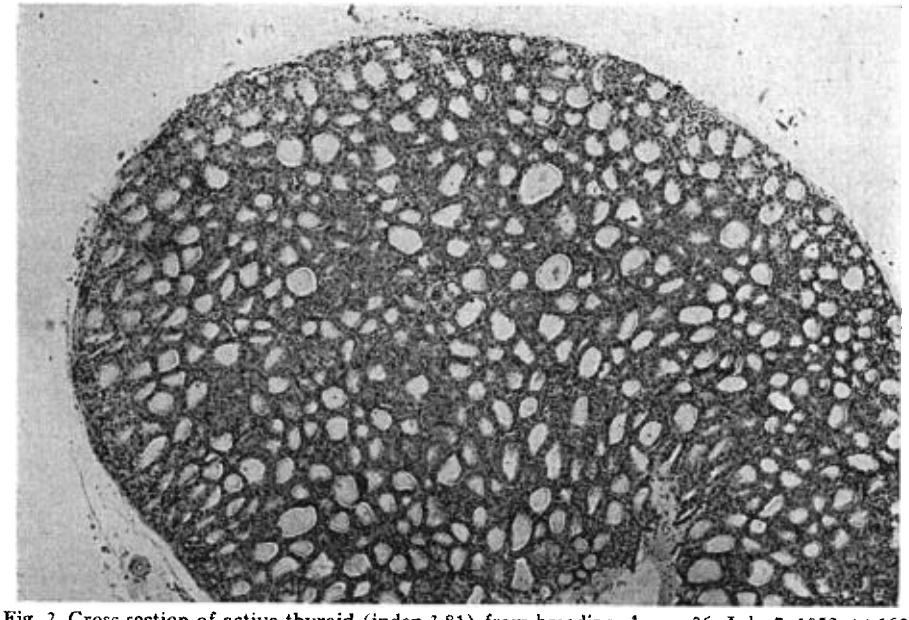

Fig. 2. Cross section of active thyroid (index 3.81) from breeding ♂, no. 26, July 7, 1952, × 162.

1. An ocular with a crosshair was oriented so that the hair passed across the middle of a given section. 2. The first and last cells of each follicle, or edge of follicle, intersected by the crosshair were then examined and assigned to one of the epithelial stages previously described. 3. The total number of cells assigned to each stage was then multiplied by the number of that stage (1, 2, 3, 4, or 5), and the figures thus derived were

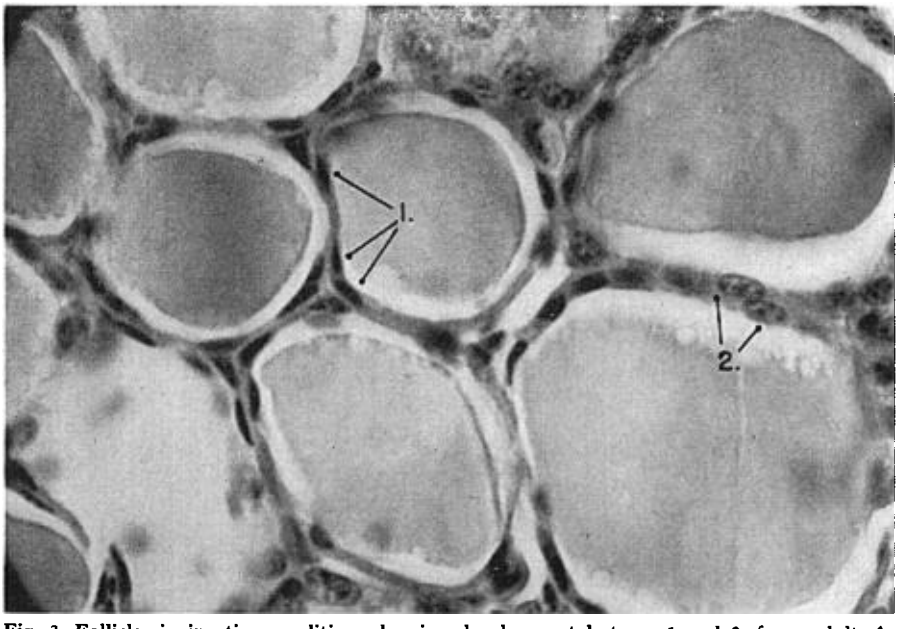

Fig. 3. Follicles in inactive condition, showing developmental stages 1 and 2, from adult ♂, no. 36, August 15, 1952 (index 2.18), × 1650.

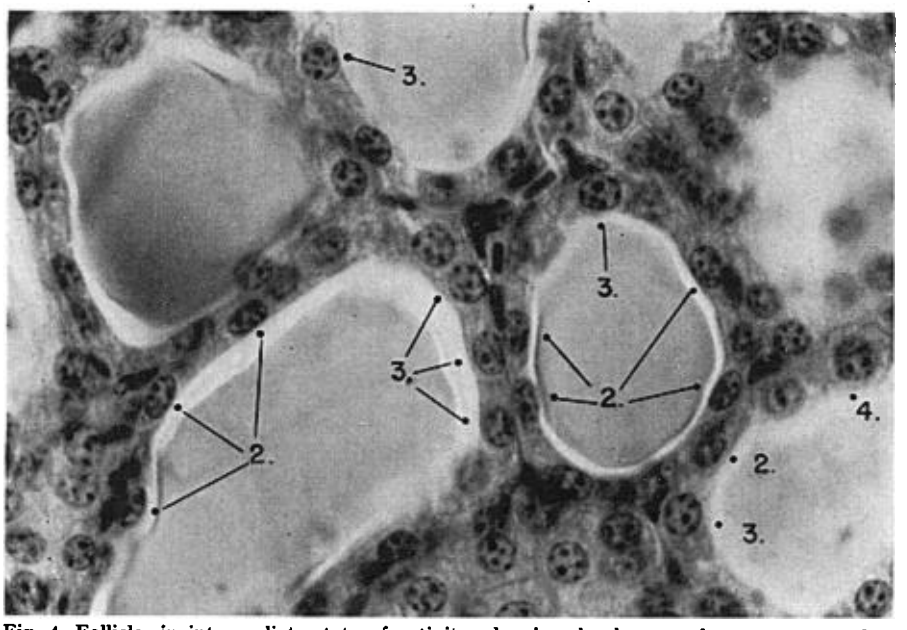

Fig. 4. Follicles in intermediate state of activity, showing developmental stages 2, 3, and 4, from immature ♀, no. 48, October 18, 1952 (index 2.80), × 1650.

added. The sum was then divided by the total number of cells examined, and an index figure for each thyroid was obtained. 4. The foregoing procedures (steps 1-3) were carried out for each of two perpendicular axes crossing the middle of each section. A lapse of over a month's time was allowed between the evaluation of the two axes to

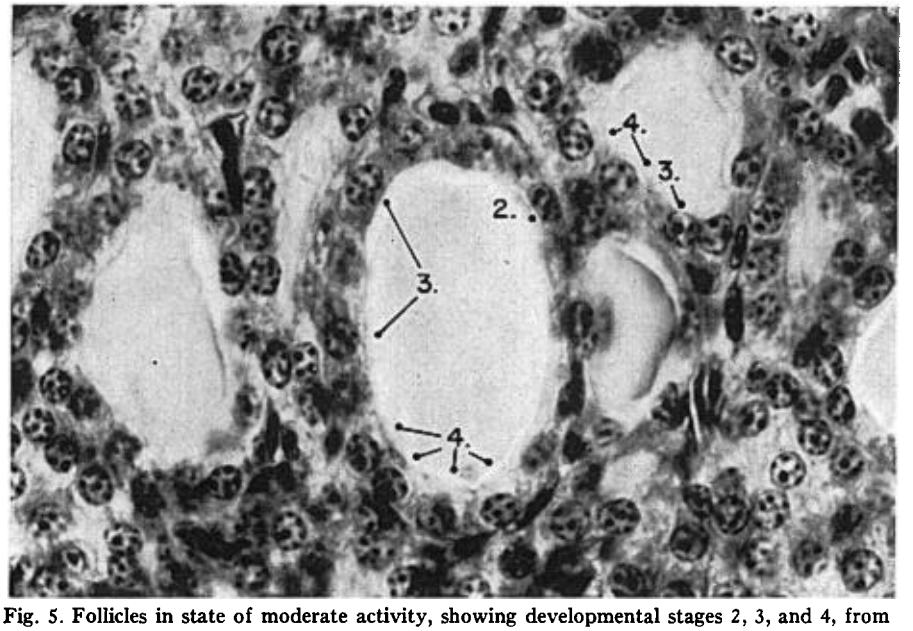

Fig. 5. Follicles in state of moderate activity, showing developmental stages 2, 3, and 4, from breeding ♂, no. 26, July 7, 1952 (index 3.81), × 1650.

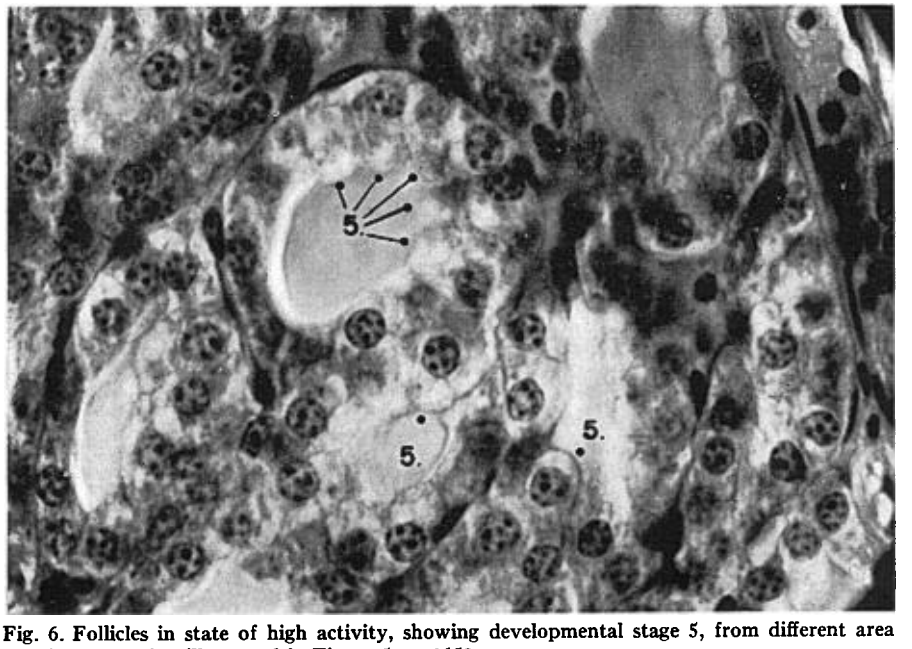

Fig. 6. Follicles in state of high activity, showing developmental stage 5, from different area of same section illustrated in Figure 5, × 1650.

avoid chance of bias. The two sets of figures (as derived in step 3) were then combined and averaged to provide the indices of thyroid activity presented in figure 9.

According to this system of evaluation, a figure of 1 would indicate a thyroid that is wholly inactive, and a figure of 5, one that is completely active. Left and right thyroid

lobes were not separated in this study, but a check on possible discrepancies between lobes, based on the examination of both lobes from 18 thyroids, indicated that no significant discrepancies occurred. It is thoroughly realized that a true determination of thyroid activity would depend on many more factors and more complicated techniques than those employed here. We believe, however, that the method used, although admittedly somewhat subjective, does serve to indicate periods of relative activity and inactivity in the thyroid cycle of the English Sparrow.

THE GONAD CYCLES

The male cycle (fig. 7).—Between June 3 and September 7, 1952, the testis cycle was based entirely on birds with fully ossified skulls. The testes of 12 males taken be-

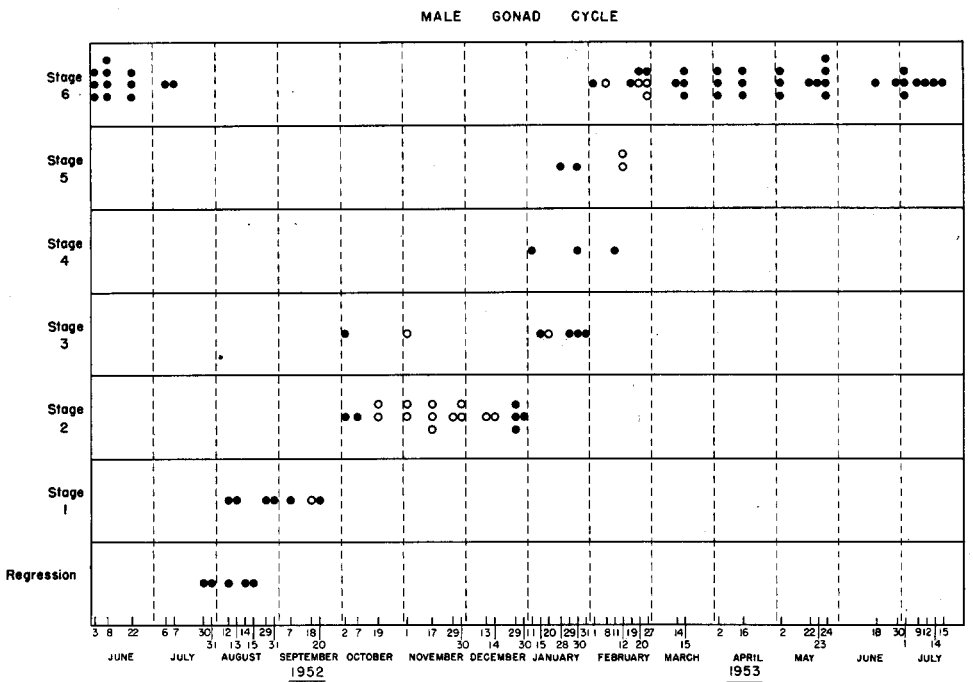

Fig. 7. Testis cycle of *Passer domesticus* at Pasadena, California, from June 3, 1952, to July 15, 1953. Dots represent individuals with completely ossified skulls; circles, individuals with partly ossified skulls.

tween June 3 and July 7 were in breeding condition (stage 6). Free spermatozoa were noted in the lumina of the tubules of most of these testes. The testes of a male trapped on July 30 were regressing from breeding condition. Two or more rows of spermatogonia were present in the tubules, but later stages were absent and the lumina were occluded. The tubules were small, the intertubular "connective tissue" elements were prominent, and the tunica albuginea was very thick. The testes of a male taken on July 31 were in an earlier stage of regression. In some tubules the spermatozoa were no longer aggregated in bundles, and the lumina were filled with free spermatozoa and degenerating cells. Of the testes of five birds trapped between August 12 and 15, three were regressing from breeding condition, and two had reached the fall inactive condi-

tion (stage 1) characterized by small tubules with one or two rows of resting spermatogonia regularly arranged around the basement membrane, prominent intertubular elements, and a very thick tunica albuginea. The testes of four adults and one immature trapped between August 29 and September 20 were also in stage 1. Leydig cells were present, but rare, in the testes of four of the seven birds in stage 1. The testes of three adults trapped between October 2 and 7 show definite signs of a recrudescence of gonadal activity. The testes of single adults trapped on October 2 and 7 were in stage 2. The spermatogonia had proliferated and were arranged irregularly, some having pushed toward the centers of the tubules. Occasional primary spermatocytes were present. A second adult caught on October 2 had testes in stage 3, with primary spermatocytes common. Leydig cells were fairly common in the testes of all three birds. This recrudescence corresponds to that reported by Riley (1937) for the English Sparrow in Iowa.

Between October 19 and December 14 the testis cycle was based entirely on immature birds with partly ossified skulls. The testes of 12 out of 13 males trapped between these dates were in stage 2. They were small, ranging from 1.0 to 2.5 mm. in greatest diameter. The testes of a single male trapped on November 1 were in stage 3. There was some variation in the testes in stage 2, since primary spermatocytes were more common in some than in others. However, the spermatogonia in all were arranged in irregular fashion about the periphery of the tubules and extended farther toward the center than in testes in stage 1. Leydig cells were present in all, ranging from rare to fairly common. Thus, in no individual were the testes in the state of complete tubular inactivity characteristic of stage 1. It is probable that there was an upswing in gonadal activity in the immatures in October and November, since the testes of a single immature trapped on September 18 were in stage 1. This upswing would account for the fact that the testes of immatures caught during the fall were in stage 2. The fact that testes taken as late as December 14 were also in this stage of activity indicates that the fall upswing was not followed by regression to the inactive state. The bill colors of the immatures trapped between October 19 and December 14 indicate that the testes of these birds were somewhat active. The bills of seven ranged from gray to dark gray, two were grayish brown, three were dark brown, and only one was the light brown color indicative of sexual inactivity.

By the end of December, skull ossification was complete in most immatures, and the skulls of these birds could not be distinguished from those of adults. Therefore, after December 29 only birds with partly ossified skulls were classed as immature.

The testes of four males trapped on December 29 and 30 were in stage 2. There was a marked increase in gonadal activity between the end of December and the middle of January. The testes of a male trapped on January 11, 1953, were in stage 4, a few spermatids being present. The left testis of this bird measured 5×3.5 mm., the right 4×4 mm. This was a sharp increase in dimensions over testes taken from October through December, which ranged between 1.0 and 2.5 mm. in greatest diameter. The testes of single males trapped on January 15 and 20 were in stage 3. The length of the left testes of these birds was 3.5 and 3.0 mm., respectively. The testes of a male trapped on January 28 were in stage 5, with some spermatids transforming into spermatozoa. The left testis measured 7×5 mm., the right 6×5 mm. The testes of five males trapped between January 29 and 31 were in stages 3, 4, and 5. The testes of a male trapped on February 1 were in early stage 6. Spermatozoa were abundant, mainly aggregated into bundles. Bundles were still being formed in some tubules. Free spermatozoa were present in the lumina of some tubules. The left testis measured 8×5 mm., the right testis 6×6 mm. An immature male trapped on February 8 had testes in stage 6. Each testis measured

7×6 mm. No spermatozoa were present in the lumina. The testes of three males trapped on February 11 and 12 were in stages 4 and 5. Two of these birds were immature. From February 19 to the end of the study on July 15, the testes of all males were in breeding condition (stage 6).

Davis (1953) reported trapping three sexually mature juvenal male English Sparrows in the Pasadena area on June 21, June 22, and July 6, 1952. These birds were characterized by incomplete skull ossification, predominantly juvenal plumage, testes which were histologically in stage 6, and dark bill coloration. Three additional sexually mature juveniles were trapped in 1953, on June 18, June 22, and July 15. Skull ossification was incomplete in all three and the plumage was predominantly juvenal, although the postjuvenal molt was under way in all. The bills of the two birds trapped in June were black. The bill of the bird taken in July was dark brown above and horn color tipped with dark brown below. The testes of all were in stage 6. Leydig cells were present, the tubules were large, and the tunica albuginea was thin and fibrous. These testes were indistinguishable from those of breeding adults. The occurrence of a few sexually precocious male juveniles is apparently regular from year to year in the Pasadena area.

The female cycle (fig. 8).—The female reproductive cycle was based on macroscopic observation only. The criteria used were follicular enlargement, increase in the size of the oviduct, and the presence or absence of a brood patch. Eleven females with fully ossified skulls, trapped between June 3 and July 9, 1952, were in breeding condition. All had brood patches and expanded oviducts. Three had large, yolky ova at the proximal end of the oviduct. Five females trapped between August 8 and September 27 were

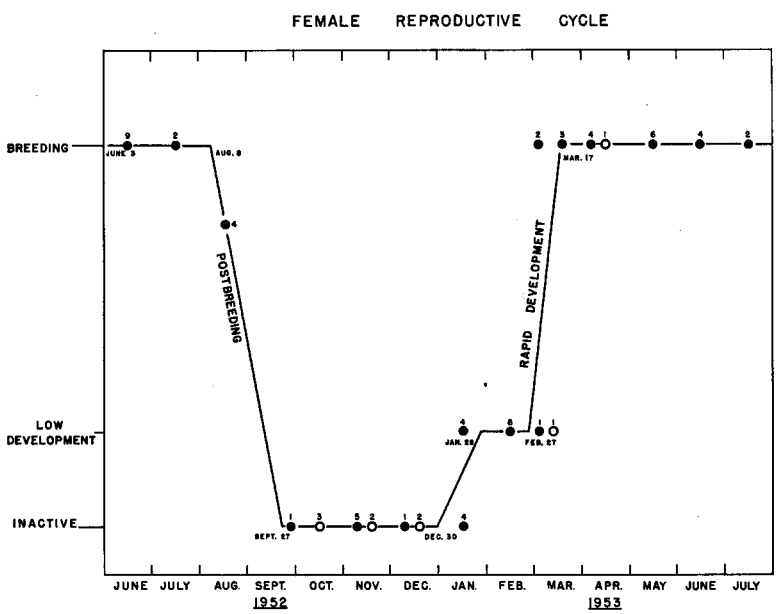

Fig. 8. Female reproductive cycle of *Passer domesticus* at Pasadena, California, from June 3, 1952, to July 15, 1953. Numbers over dots represent total numbers of birds with ossified skulls taken each month in the various stages of reproductive activity; numbers over circles represent the data for birds with partly ossified skulls. Dates on chart refer to approximate times of changes in the reproductive cycle.

in postbreeding condition. A female taken on August 29 had a few ensheathed replacement feathers in the brood patch. Females taken between September 27 and December 30 were sexually inactive. The ovaries of these birds appeared almost homogeneous, with all follicles small and about the same size. Two females were trapped on January 1, 1953. The ovary of one was inactive, but a few slightly enlarged follicles were present in the ovary of the other. The ovaries of females taken between January 1 and 28 were either inactive or in a stage of low development as evidenced by the slight enlargement of some follicles. Between February 1 and 27 enlarged follicles were present in the ovaries of all females examined. Three of eight birds collected during this period had noticeably enlarged oviducts. Between February 27 and March 17 there was a rapid development of the reproductive tract to breeding condition. Of three females trapped on March 14, two were in breeding condition. Each had a brood patch and greatly enlarged oviduct. The ovary of one had two large, yolky ova measuring 7 and 8 mm. in greatest diameter, and a large, soft egg was present in the terminus of the oviduct. The ovary of the other had many enlarged follicles and a yolky ovum 4 mm. long. The ovary of a bird killed on March 16 was still in a low stage of development. Of three birds trapped on March 17, two were ready to lay, and the ovary of the third contained two yolky ova 7 and 9 mm. long. All the females taken after March 17 were in breeding condition.

The females thus progressed from a low stage of ovarian development to breeding condition during a period of 18 days. This rapid development is similar to that described for other passerines (for example, *Sturnus vulgaris,* Bissonnette and Zujko, 1936; *Junco oreganus,* Wolfson, 1942).

THE THYROID CYCLE

In working out the thyroid cycle, immatures and adults were not separated. During the fall and early winter, when these age groups can be distinguished on the basis of degree of skull ossification, the males in each age group are showing signs of slight gonadal upswing and all females are sexually inactive. Therefore the thyroids in each age group are subjected to the same influences.

The thyroids of the males showed a steady rise in activity from June 3 to July 30, 1952. This rise in activity apparently represented the premolt activity period of the thyroid, since molt in the population studied extended from August 13 to September 18. Between July 31 and August 29 there was considerable variation in thyroid activity. This did not seem to be correlated with the stage of molt of individual birds. Two males taken on August 12 had not started the molt, but their thyroids were active. A male taken on August 13 had replaced the inner primaries on each side, and the thyroid of this bird was also active. Single males trapped on August 14 and 15 had not started the molt, and their thyroids were inactive. A male taken on August 29 was in the terminal stage of molt, and the thyroid was active. Apparently there was considerable individual variation in the rate of regression from the premolt level of activity. During September thyroid activity was noticeably below the premolt level.

From October 2 to November 1 there was a steady rise in thyroid activity. This rise coincided with the first noticeable drop in air temperatures from the high temperatures of the preceding three months which had reached a peak in September (fig. 10). However, in November there was a decrease in thyroid activity even though air temperatures continued to drop during that month. Although the temperatures dropped even lower than those in October, apparently they never became low enough to sustain the higher level of thyroid activity which had been induced in October as a response to the initial lowering of air temperatures. The fact that the only marked deposition of subcutaneous

fat in males that occurred during this study took place between October 19 and November 30 would indicate that the relatively mild temperatures of that period reduced the necessity for high thyroid activity. Of 11 males trapped between these dates, four had fat deposits which ranged from moderately heavy to heavy. This suggests that the intake of productive energy exceeded the demand for such energy and the excess was stored as fat. In October and November energy was not expended in reproductive activity, and temperatures were not low enough to demand increased utilization of energy for the maintenance of body temperature. The situation seems similar to the one hypothesized by Kendeigh (1949) to account for the deposition of fat in migratory birds prior to the spring migration. The fact that the major period of fat deposition in females occurred during the same period further supports the explanation just suggested. Of ten females trapped between October 19 and November 29, five had moderately heavy to heavy fat deposits. The only other females with appreciable fat deposits were single birds trapped on February 21 and March 17. Since fat was deposited in both sexes at a time when the testes were somewhat active but the ovaries were completely inactive, it would appear that accumulation of fat was not correlated with gonadal activity.

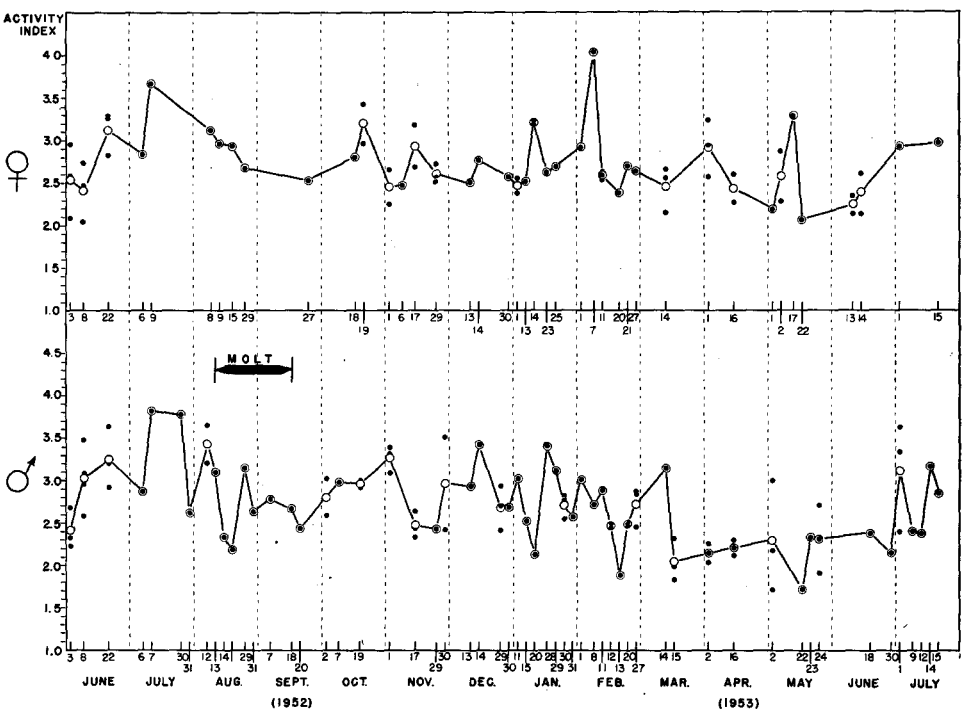

Fig. 9. Thyroid cycles of male and female *Passer domesticus* at Pasadena, California, from June 3, 1952, to July 15, 1953. Dots represent values for individual birds; circles represent average values when more than one individual was taken on the same day; where average value and an individual value coincide, a dot appears within the circle.

Between November 30, 1952, and March 15, 1953, thyroid activity was subject to a great amount of individual variation in the males. The abrupt peaks and lows are not explicable on the basis of external temperatures. The most important consideration is that the winter of 1952–1953 at Pasadena was unusually mild. Weekly temperatures

between November 30 and March 15, based on averages of daily maxima and minima, averaged 55.5°F. The lowest temperature during this period was 33°. On 26 days the maxima were 75° or above. On 42 days the minima were 45° or above. It seems likely that the intensity of the stimulus provided by air temperature was never maintained at a level high enough, and for a sufficiently long period, to cause a sustained rise in thy-

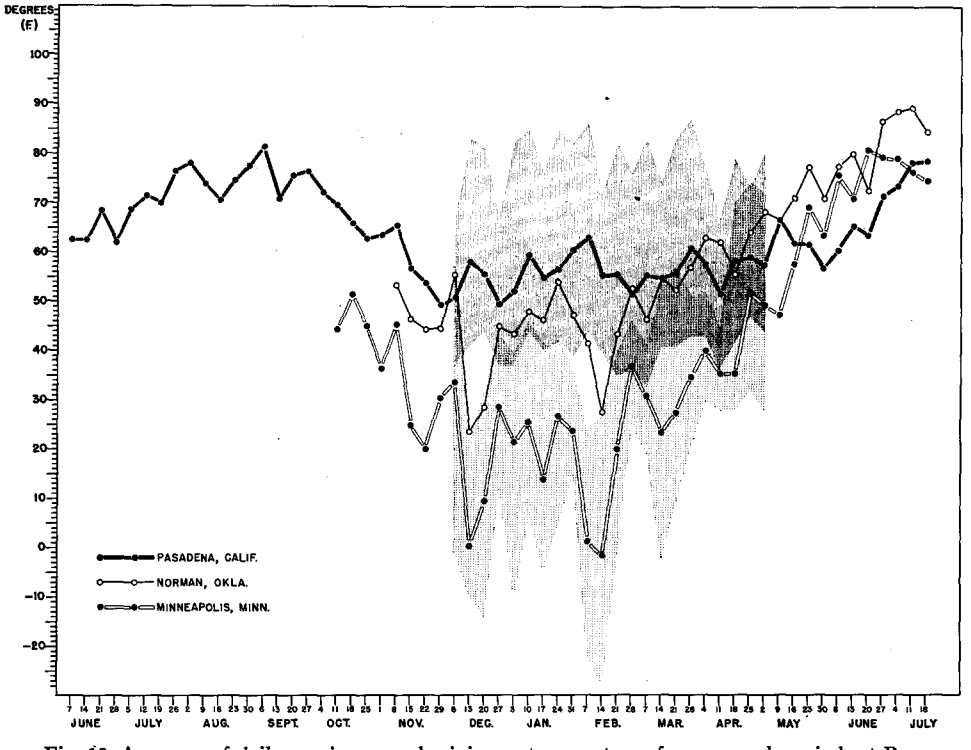

Fig. 10. Averages of daily maximum and minimum temperatures for one-week periods at Pasadena, California (June, 1952, to July, 1953), Norman, Oklahoma (November, 1932, to July, 1933), and Minneapolis, Minnesota (October, 1932, to July, 1933). Medium stippling represents total weekly temperature ranges at Pasadena; light stippling represents total weekly temperature ranges at Minneapolis; dark stippling occurs at areas of temperature overlap. Pasadena temperatures from Pasadena Water Department records; Norman and Minneapolis temperatures from U. S. Dept. Agr., Weather Bureau, Climatological Data.

roid activity in the entire male population, or even in an appreciable part of it. In short, with the environmental stimulus so weak, there was probably an expression of the individual physiological variability to be expected in a series of birds of unknown origin and past history. Between March 15 and June 30 thyroid activity was at a noticeably low level. Between July 1 and 15 there was again considerable variation, but the level of thyroid activity during this period was definitely above that noted during the preceding three and one-half months. This apparently represented the onset of premolt thyroid activity in 1953.

The study of the female thyroid cycle was less satisfactory since only 64 birds were examined as against 91 males. In the females there was an almost steady rise in thyroid activity between June 3 and July 9, 1952, apparently representing the premolt activity. Between July 9 and September 27 there was a gradual, steady drop-off in activity, fol-

lowed by a gradual rise until October 19. Between October 19 and May 22 the cycle was variable, although generally within narrower limits than in the male cycle. Between May 22 and July 15 there was a steady rise in thyroid activity, probably representing the premolt activity of 1953. A summary of the male and female thyroid cycles is presented in figure 9.

DISCUSSION

The gonad cycles.—Blanchard (1941) and Blanchard and Erickson (1949), working with various races of the White-crowned Sparrow (*Zonotrichia leucophrys*) described a stage of complete testis inactivity in which the tubules were wholly inactive and Leydig cells were absent from the intertubular tissue. This condition, termed stage 1, occurred during the fall and early winter. It was followed in late winter by stage 2, in which the tubules were still inactive but occasional Leydig cells appeared in the intertubular tissue. Wolfson (1942) did not recognize a stage in the testis cycle of the Oregon Junco (*Junco oreganus*) corresponding to stage 1 of Blanchard. He noted that when the tubules were inactive and the size of the testis was at a minimum the intertubular tissue contained two types of cells, one of which he regarded as interstitial cells. More recently A. H. Miller (1954), working with *Zonotrichia leucophrys* and with the Golden-crowned Sparrow (*Zonotrichia coronata*), reported that testes of these species examined during the refractory period were rarely found without either Leydig cells, or somewhat enlarged and rounded cells that might be developing Leydig cells. Our material supports the findings of Wolfson and Miller. As mentioned previously, four of seven testes of *Passer domesticus* in stage 1 taken between August 12 and September 20 showed occasional Leydig cells in the intertubular tissue. In our material we could make no clear-cut distinction between stages corresponding to stages 1 and 2 of Blanchard.

Wolfson (*op. cit.*) recognized five histologic stages in testis development in *Junco oreganus*. Our stages 1 to 3 correspond to his stages of similar designation. His stage 4 includes our stages 4 and 5. He pointed out that between stage 3 and breeding condition events occur with such rapidity that it is not feasable to recognize more than one stage during this period. Our stages 4 and 5 were the most difficult to delimit. However, they were kept apart to show in more detail the relative positions of individuals in the gonad cycle and the amount of variation in testes taken on the same day. The fact that we recognize six stages in *Passer domesticus* does not imply any marked difference between the testis cycles of this species and *Junco oreganus* but merely reflects a difference on the part of the investigators in the arbitrary and subjective breakdown of a rapid and continuous process.

The testis cycle at Pasadena differed in several respects from the cycles of the English Sparrow described from Norman, Oklahoma, by Allender (1936*a*, 1936*b*) and from Minneapolis-St. Paul, Minnesota, by Kirschbaum and Ringoen (1936). Allender (1936*b*) reported the absence of interstitial cells in testes in stage 1, whereas we found such cells present in more than half of the testes in this stage. She stated that when the tubules enlarge and spermatogenesis is under way "very few interstitial cells are present and for a short time only." In our material these cells are present in all stages from 1 to 6. She also stated that "no spermatozoa were found free in the lumen at any time" in testes in breeding condition. This is in marked contrast to our findings, since the majority of testes in breeding condition had free spermatozoa in the lumina. Neither Allender (*op. cit.*) nor Kirschbaum and Ringoen (1936) reported any signs of autumnal gonadal activity in adults or first-year birds. We noted a definite upswing in gonadal activity in both age groups in October and early November, following which the testes failed to regress to the inactive condition of the late summer and early fall. Our findings

agree more closely with those of Riley (1937) who reported increased gonadal activity in males of this species in Iowa during November, soon followed by regression to the completely inactive state. Marshall (cited in Summers-Smith, 1954) reported that gonadal development had begun in eight male *Passer domesticus* taken in late October and early November in southern England. Daanje (cited in Summers-Smith, 1954) in The Netherlands and Summers-Smith (*op. cit.*) in England noted that communal displays involving a single unresponsive female and two or more males with active testes decreased in frequency in the late summer and became more frequent in October and November. These observations suggest increased gonadal activity in the males during these months. Allender (1936*a*) reported that at Norman both sexes came into breeding condition at about the same time, March 1. At Pasadena the males reached breeding condition almost a month ahead of the females (February 19 versus March 17). At Minneapolis-St. Paul, Kirchbaum and Ringoen (1936) reported that the males reached breeding condition at the end of March. At this time large follicles were present in the ovary. The oviducts were hypertrophied but "not until April, however, do they appear ready to receive discharged egg cells." A lag in the female cycle is thus implied, although it is not possible to estimate its magnitude.

The possible influence of the thyroid cycle on the testis cycle.—The males reached breeding condition at Pasadena on February 19, at Norman, Oklahoma, on March 1, and at Minneapolis-St. Paul, Minnesota, on or about March 31. Pasadena lies at about latitude 34° 05′, Norman at 35° 10′, and Minneapolis-St. Paul at 45°. Thus the differences in the timing of testis development at the three localities were roughly proportional to the differences in latitude. Between Pasadena and Norman there is a difference of 10 days between the testis cyles and a difference of 1° 05′ in latitude, between Norman and Minneapolis-St. Paul, 30 days and 9° 50′, and between Pasadena and Minneapolis-St. Paul, 40 days and 10° 55′. Since the daylength cycle is retarded from south to north before March 20, a partial correlation may be made between daylength and gonadal activity. The latitudinal difference between Pasadena and Norman is so slight that the daylength cycles would be about the same at each locality, and difference in daylength could account for only a small part of the total difference between the testis cycles. However, there is a marked difference between the daylength cycles at Pasadena and Minneapolis-St. Paul, but it is difficult to estimate the amount of this difference as the daylength cycles are of different configuration.

In order to arrive at a standard for comparison, the ten-hour day, based on civil sunrise to civil sunset, may be used as an arbitrary point in the daylength cycle. The ten-hour day is reached at Pasadena on January 12, and at Minneapolis-St. Paul on February 6. This represents a difference of 25 days. To give some idea of the events in the testis cycle occurring at each locality near these dates, a single male taken at Pasadena on January 11 was in stage 4, and one taken on January 15 was in stage 3. At Minneapolis-St. Paul, some testes taken on February 12 were in transition from stage 1 to stage 2. Other testes taken on the same date were in stage 1 with some proliferation of spermatogonia. Daylength is the same at both localities on March 20. At this time the males at Pasadena had been in stage 6 for a month. The testes of males collected at Minneapolis-St. Paul on March 19 showed metamorphosing spermatids and a few spermatozoa (stage 5). "However, a testis with great numbers of mature spermatozoa is not observed until March 26" and not all testes were producing mature spermatozoa at that date (Kirschbaum and Ringoen, 1936).

Again using the ten-hour day as a reference point, the males at Pasadena came into breeding condition on February 19, 38 days after this daylength had been reached.

At Minneapolis-St. Paul they reached breeding condition on March 31, 53 days after the ten-hour day had been reached. Daylength at Pasadena on February 19, when the males reached breeding condition, was 11 hours and 3 minutes. Daylength at Minneapolis-St. Paul on March 31, when the males there reached breeding condition, was 12 hours and 41 minutes. It would appear that some factors other than the difference in the daylength cycles were retarding the testis cycle at Minneapolis-St. Paul. Some factor other than daylength must definitely have been involved in delaying the cycle at Norman by ten days, since the latitudinal difference between Pasadena and Norman is so slight.

Using the ten-hour day as a reference point, 25 of the total difference of 40 days between the testis cycles at Pasadena and Minneapolis-St. Paul may be accounted for on the basis of daylength. This leaves a difference of 15 days to be accounted for. As pointed out previously, it took the males at Pasadena 38 days to reach breeding condition after the ten-hour day had been reached, whereas it took the males at Minneapolis-St. Paul 53 days after this point in the daylength cycle. This again is a difference of 15 days. As regards the difference between the testis cycles at Pasadena and Norman, it may be assumed that the entire difference of ten days is independent of daylength since the two localities are at approximately the same latitude. Thus there is a greater proportional difference between the cycles at Pasadena and Minneapolis-St. Paul than between the cycles at Pasadena and Norman, 15 versus 10 days. Since the differences of 10 and 15 days in the testis cycles are apparently independent of daylength, another environmental factor must be proposed to account for them.

When the temperatures at the three localities are plotted (fig. 10), it may be seen that during the critical months of the testis cycle (January, February, and March), temperatures at Norman are lower than those at Pasadena and they are considerably lower at Minneapolis than at either of the other localities. A correlation may then be made between the differences in temperature and the differences in the timing of the three testis cycles. The retarding effect of low temperature on spermatogenic activity has been reported in several species of birds. For example, Marshall (1951) collected the testes of four species of passerines common at Oxford, England, in mid-March, 1947, during one of the coldest winters on record in the British Isles. Testes of the same species were collected at precisely the same locality exactly one year later, during an unusually mild winter. The testes collected in 1947 were in a low stage of development, whereas those collected in 1948 were far advanced. Blanchard (1941) noted a high correlation between temperature and variations in the timing of the testis cycle in a population of *Zonotrichia leucophrys nuttalli,* a resident form, studied at Berkeley, California, over a five-year period. It seems obvious that low external temperatures must have affected some aspect of the physiology of these birds in such a way that spermatogenic activity was retarded.

The experimental induction of high thyroid activity in *Passer domesticus* by the exposure of individuals to low temperatures (D. S. Miller, 1939), and the fact that thyroid activity increases in wild birds during the cold months of the year (see Höhn, 1950), at once suggests that the thyroid may be involved in the effect of low temperatures on the gonad cycle. The thyroids of the sparrows caught at Pasadena during the mild winter of 1952–1953 showed great individual variation from January to mid-March, and at no time during this critical period in the testis cycle was there a prolonged period of high thyroid activity. Kirschbaum and Ringoen did not examine the thyroids of *Passer domesticus* at Minneapolis-St. Paul, but in view of the far lower winter temperatures at that locality it seems likely that the thyroids of their sparrows would be more active

than the thyroids of the sparrows taken at Pasadena. Winter temperatures were higher at Norman than at Minneapolis, but averaged 9°F. lower than the temperatures at Pasadena during January, February, and March. During these months, it seems possible that the thyroids of the birds at Norman would be somewhat more active than those of the birds trapped at Pasadena and less active than those of the birds taken at Minneapolis-St. Paul. If this be true, the increase in postulated thyroid function from Pasadena to Norman and from Norman to Minneapolis-St. Paul would correlate with the otherwise unexplained differences of ten days between the testis cycles at Pasadena and Norman, and 15 days between these cycles at Pasadena and Minneapolis-St. Paul.

It is here suggested, therefore, that thyroid function, as influenced by winter temperature, may account, at least in part, for temporal differences in the testis cycles of populations of the same species subjected to different winter temperatures, whether at one locality from year to year, or at different localities within the same year. There are two ways in which thyroid function might affect the testis cycle. First, the thyroids and the testes are both controlled by hormones of the anterior pituitary. It is possible that the thyrotrophic and gonadotrophic functions of the pituitary are antagonistic. If this be so, the pituitary is subjected to two environmental stimuli during the late winter that are of major importance in this regard. One is external temperature, inducing thyrotrophic activity, and the other is increasing daylength, inducing gonadotrophic activity. With relatively high winter temperatures, as at Pasadena, the thyrotrophic function of the pituitary would be minimized and gonadotrophic function would be induced in response to the daylength cycle, unhampered by thyrotrophic activity. The reverse would be true in the Minneapolis-St. Paul area, where a high level of thyrotrophic function would be induced by low winter temperatures, and gonadotrophic function would be minimized. An intermediate situation would be found at Norman. Second, it is possible that the high level of thyroxin resulting from high and prolonged thyroid activity, maintained by a lengthy period of low winter temperatures, would in itself have a depressant effect on spermatogenic activity.

It seems likely that the concept of the testis cycle, traditionally thought of in terms of daylength-anterior pituitary-testes, represents an oversimplification. It does not seem possible to divorce the anterior pituitary and the testes from the rest of the endocrine system, nor does it seem possible to divorce daylength from the myriad of other environmental factors which are of utmost importance to birds living under natural conditions. It is hoped that critical experimental work will in the future assess the effects of low temperatures and of such organs as the thyroid and adrenals on the testis cycle.

It seems obvious that the three testis cycles discussed in this paper were controlled by factors other than an inherent annual rhythm. If an inherent, genetically controlled, annual rhythm were invoked to account for the differences in the timing of the three cycles, we would have to assume that each of the three populations concerned differed genetically from the other two, and that we are dealing with three physiological subspecies. However, *Passer domesticus* was introduced into the United States less than 100 years ago, and has subsequently invaded nearly all parts of the country, flourishing over a wide range of environmental conditions. It is inconceivable that this, or any other avian species, should have evolved within such a short period of time a plethora of populations, each adapted by a genetically controlled inherent annual rhythm to the conditions present within its range. It seems impossible to escape the conclusion that geographic variation in the tesis cycle results from the geographic variation of certain environmental conditions. Once under way, from whatever cause, the sequence and timing of events in the testis cycle must be regulated by such external factors as daylength and temperature, to name only two.

The timing of breeding.—At Pasadena the actual onset of breeding occurred about one month after the males had reached breeding condition. At the time that the testes were producing mature spermatozoa, ovarian development was still slight. The breeding time was therefore established for this population by the ovarian cycle, not by the testis cycle. The factors influencing the ovarian cycle in birds are not well understood. Summers-Smith (1954) is of the opinion that communal displays in which several male English Sparrows in breeding condition pursue a non-responsive female may be of importance in bringing the female into breeding condition. We have no evidence of this phenomenon and its effect on the females, but it seems likely that the changes in male behavior resulting from gonadal activity at a time when the female reproductive tract is almost inactive are important as a stimulus to the female cycle in this species.

The finding of Allender (1936*a*) on *Passer domesticus* at Norman indicate that there may be some variation among populations in the temporal difference between the male and female cycles. She reported that at Norman both sexes came into breeding condition at the same time, about March 1. This was based on histological examination of testes, the time of mating, building, and incubating in the population, and the report of week-old young at Norman on March 20 by Nice (1931).

The importance of the female cycle to the timing of actual breeding in a population of birds cannot be overemphasized. Marshall (1951) noted, in his observations of passerines at Oxford, previously discussed, that although the testis cycles of the four species investigated during the severe winter of 1947 were noticeably retarded, "the hard winter was followed by an abnormally bright spell (after the collection date)" and "the surviving birds of at least three species bred at about the normal time!" He felt that unless some dietary factor was involved, sunshine and temperature must have been especially important in the timing of the cycle. An alternative explanation is that the breeding times of these three species were set by the ovarian, rather than by the testis, cycle, and any temporal disparity between the male and female cycles was probably cut down or obliterated by the retardation of the male cycle. In this same paper Marshall cites several examples of the influence of the ovarian cycle in delaying the timing of breeding in populations of several species of birds in which the males were in breeding condition. The timing of breeding of *Passer domesticus* at Pasadena was evidently regulated in the same fashion.

SUMMARY

The gonad and thyroid cycles of *Passer domesticus* were established for the population at Pasadena, California, from June 3, 1952, to July 15, 1953.

The males were in breeding condition in June and early July, 1952, and regressed to an inactive gonadal state in the late summer and early fall. An upswing in gonadal activity occurred in October and November, followed by incomplete regression. Increased spermatogenic activity started in January, 1953, and the males reached breeding condition by February 19, 1953.

The females were in breeding condition in June and early July, 1952. They were in postbreeding condition from early August to late September. The ovary was completely inactive from the end of September to early January, 1953. A low stage of ovarian development was noted from January to the end of February. Rapid development of the reproductive tract took place between the end of February and the middle of March, and the females reached breeding condition by March 17, 1953.

The thyroid cycle was similar in the two sexes. The thyroids were active prior to the onset of molt in 1952 and 1953. Thyroid activity was highly variable during the winter months. The absence of a prolonged period of high thyroid activity in winter was probably the result of the mildness of the winter of 1952–1953 at Pasadena.

In comparison with the testis cycles of this species described from Norman, Oklahoma, and Minneapolis-St. Paul, Minnesota, the males at Pasadena reached breeding condition 10 days before the males at Norman and 40 days before the males at Minneapolis-St. Paul. These differences cannot be explained solely on the basis of the differences in the daylength cycles occurring at each locality.

Winter temperatures at Pasadena were relatively high, those at Norman lower, and those at Minneapolis-St. Paul even lower. There is a correlation between winter temperature and the time at which the males at the three localities reached breeding condition.

Since low temperatures induce high thyroid activity in the English Sparrow, it is suggested that part of the difference in the timing of the testis cycles at the three localities might be the result of interference of the temperature-pituitary-thyroid cycle with the daylength-pituitary-testis cycle. This might result from a possible antagonism of the thyrotropic and gonadotrophic functions of the pituitary, or from the high level of thyroxin maintained by thyroids which were highly active over a prolonged period as a result of low winter temperatures.

Since the males at Pasadena came into breeding condition one month earlier than the females, the time of actual breeding in the population at Pasadena was set by the ovarian rather than by the testis cycle.

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