THE ANNUAL CYCLE OF THYROID ACTIVITY IN WHITE-CROWNED SPARROWS OF EASTERN WASHINGTON

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It is now evident that many species of plants and animals have long period physiologic cycles. In birds, the most striking of these cycles have a period of one year. Familiar examples are the annual cycles in organs associated with reproduction and migration (Farner, 1955, 1958, 1959). Less familiar are the annual cycles in such organs as the liver (Oakeson, 1953) and the thyroid gland (Höhn, 1950) whose relation with reproduction or migration is not clear.

Some annual physiological cycles are caused by cyclic factors in the environment. For instance, day length has been demonstrated to be the main cause of the annual occurrence of testicular development in certain passerine birds (Farner, 1959). On the other hand, internal mechanisms have been suggested to be the sole cause of some physiological cycles including annual cycles (Webb and Brown, 1959).

The present paper is concerned with the annual cycle of thyroid activity in a passerine species. Despite the many investigations of annual cycles of thyroid activity in passerine birds, there is still no agreement concerning the form of a typical thyroid cycle. Our first objective, necessarily, has been a quantitative description of the principal features of the thyroid cycle in the bird selected for investigation, *Zonotrichia leucophrys gambelii,* a race of the White-crowned Sparrow. This race and other representatives of the genus *Zonotrichia* have already been used for many studies of annual physiological cycles. A good opportunity was thereby provided to examine the relation of the thyroid cycle not only to cyclic environmental factors but also to other physiological cycles. Evidence has been obtained which suggests that the thyroid cycle in *Z. l. gambelii* is caused mainly by a cyclic environmental factor, very probably temperature.

While our investigations were in progress in Washington, somewhat similar studies were carried out independently on the same race in California and Alaska by Oakeson and Lilley (1957, 1960). This now permits an important series of comparisons.

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MATERIALS AND METHODS

Birds used.—The birds involved in this investigation, except two mentioned later, were obtained in the southeastern part of Whitman County, Washington (latitude 46°N). They were taken either from a wintering population near Wawawai in the Snake River Canyon or from migrating flocks near Kamiak Butte. Eighteen samples, a total of 100 birds, were used to determine the course of thyroid activity through the year. Of these, 75 birds were caught with mist nets from September 29, 1955, to May 5, 1956. They were weighed in the field and brought alive to the laboratory where they were killed. Both thyroid glands were removed and preserved. Observations at the time of death were made also on body weight and molt. The gonads were preserved for weighing as described by Farner and Wilson (1957).

The interval between capture and death was usually from 3 to 10 hours, but in certain instances, noted later, the birds were kept for a few days in outdoor aviaries (4×2.7×2 meters) where they were exposed to conditions of lighting and temperature natural for the locality. To test whether the 3-to 10-hour period between capture and death affected thyroid activity, an additional group of 10 birds was captured on January 2, 1957. The thyroids were removed from four of these birds at the time of capture for comparison with the thyroids of the remaining six birds which were killed six hours later at the laboratory.

Information about the state of the thyroid gland in summer was obtained from two sources: (1) Two breeding birds which were shot on July 15, 1956, near Hart's Pass, Okanogan County, Washington (elevation about 7000 ft., latitude 49°N). (2) Thirteen birds which were caught during the winter of 1954–1955 and kept in the outdoor aviaries until the summer of 1955.

During maintenance of birds in the outdoor aviaries, under the same conditions observed by Farner and Wilson (1957), a nutritionally adequate, chick-starter mash and water were always available. The body weight and testicular development of birds under these conditions does not differ essentially from those of birds in the wild population. Also, prenuptial molt, fat deposition and migratory unrest or *Zugunruhe* occur in spring at exactly the same time as in the wild population, even if the birds are confined to small outdoor cages (King and Farner, 1956, 1959). Likewise, it has been observed by several investigators in this laboratory (unpublished) that loss of spring fat, testicular regression, postnuptial molt, autumnal fat deposition and *Zugunruhe* proceed in the same sequence as these events in the natural populations of this race studied elsewhere by Blanchard and Erickson (1949) and Oakeson (1954). It is reasonable, then, to assume that thyroid activity of such aviary birds should also reflect closely the thyroid activity of natural populations.

In addition to the description of the natural annual cycle of thyroid activity, experiments were conducted indoors under controlled conditions of lighting, temperature and nutrition in the manner described previously (Farner and Wilson, *op. cit.*; King and Farner, 1956, 1959).

Preparation of thyroids for measurement.—Both thyroid glands were removed within a few minutes after death and fixed in Bouin's mixture. They were embedded in paraffin by the conventional, alcohol-paraffin technique. Sections, 6μ thick, prepared from one or both thyroids, were mounted on slides and stained with Harris' haematoxylin and eosin. Care was taken to use exactly the same technique of preparation for all thyroid sections.

Measurement of thyroid activity.—Thyroid activity was measured by the method developed by Uotila and Kannas (1952), Tala (1952), Lever and Vlijm (1955), and Wahlberg (1955). In this method, the percentage of secretory epithelium (E%) in the gland, an experimentally tested index of thyroid activity, is measured on sections of the gland. Preliminary tests on the thyroids of White-crowned Sparrows showed that a value of E% not farther away from the true value than about 5 units could be obtained from a single section through the middle of either of the two glands. The central part of the image of such a section was projected on a piece of paper with two straight lines, each 20.0 cm. long, intersecting at right angles. The magnification of the image was 520 and the total length of tissue measured 40.0/520 cm., that is 770μ—a distance that traverses between 20 and 30 thyroid follicles in these birds.

Environmental temperature.—Semi-monthly means of the daily maximum and of the daily minimum air temperatures at the weather stations nearest the collecting areas were computed from the records for 1955–56 in the "Climatological Data" of the United

States Weather Bureau. The mean temperature for each half-month was then obtained by averaging the average daily maximum and the average daily minimum. Monthly averages, computed in an analogous way, were taken directly from these climatological data.

RESULTS

Description of the thyroid cycle.—Table 1 gives the dates for the 17 samples of birds taken for this study through the year 1955–56. The table also contains data from

Table 1

Annual Cycles of Molt, Body Weight, Migration and Testicular Weight

Date caught	Date killed	Number of birds	Number in molt	Mean body weight in grams	Number of males	Mean weight of testes in milligrams
Winter	July 30	6	6	26.6	4	2
of 1955	Aug. 27	7	0	27.1	5	2
Sept. 29	Oct. 1	6[1]	0	26.1	4	1
Oct. 6	Oct. 6	6[1]	0	28.2	2	1
Nov. 10	Nov. 10	3	0	26.4	2	1
Nov. 19	Nov. 19	6	0	26.9	4	1
Dec. 8	Dec. 8	6	0	27.3	5	1
Dec. 23	Dec. 23	3	0	29.2	3	1
Jan. 13	Jan. 13	6	0	27.6	6	1
Jan. 26	Jan. 26	3	0	27.4	3	1
Feb. 10	Feb. 10	9	0	26.1	4	1
Mar. 10	Mar. 10	6	0	26.0	6	1
Apr. 4	Apr. 4	3	3	26.2	2	5
Mar. 10	Apr. 6	3	3	29.2	3	5
Apr. 21	Apr. 21	5	1	28.3	4	13
May 5	May 5	10[1]	0	26.8	4	50
......	July 15	2	1	......	1	....

[1] Migrating.

these samples concerning several annual physiological cycles other than the thyroid cycle. The data show the cyclic nature of molt, body weight, migration and testicular weight and are in general agreement with previous data concerning these cycles in natural populations of *Z. l. gambelii* (for example, Blanchard and Erickson, 1949; Oakeson, 1954). There is reason, then, to expect that this set of samples should also provide a picture of the annual course of thyroid activity that is typical of the populations studied.

Table 2

Effect of Experience between Capture in the Field and Death in the Laboratory on Thyroid Activity (E%)

	At time of capture	Six hours later in the laboratory
Mean E%	73	75
Number of birds	4	6

Further evidence that these samples should reflect the natural state of thyroid activity is given by the results (table 2) of an experiment on an eighteenth sample of birds collected in the following winter (1956–57). The results show that the experience between capture in the field and death hours later in the laboratory does not affect thyroid activity appreciably.

The results of the thyroid measurements made on the 17 samples of birds taken in 1955–56 are presented in figure 1 (solid circles). Statistical analysis confirms what is immediately apparent by inspection, namely, that there is a marked cycle of thyroid activity through the year. According to Student's t-test, the mean value of E% for any sample of birds taken on a particular day from October through March is significantly higher than that of samples taken from May through August. When plotted against time, the sample means form a smooth curve that passes within the standard deviation of each sample mean. As the standard deviation is never very large (average coefficient of variation equals 12 per cent), it is suggested, on the grounds of simplicity, that the smooth curve is a better representation of the thyroid cycle than the irregular line that could be obtained by going through each of the sample means.

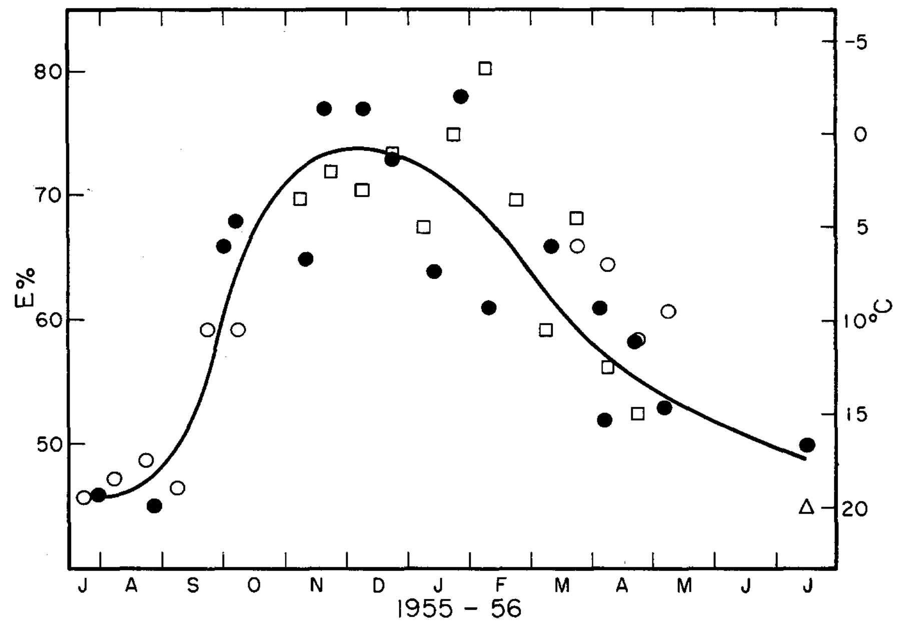

Fig. 1. Annual cycles of thyroid activity (E%) and air temperature for *Zonotrichia leucophrys gambelii* in eastern Washington. Each solid circle represents the mean thyroid activity for a sample of birds taken on a particular date. The curve has been fitted to the solid circles by eye. Half-monthly means (1st to 15th, and 16th to the end of each month) of temperature at the nearest weather station are represented by empty circles (Pullman, Whitman County), squares (Wawawai, Whitman County), and triangles (Winthrop, Okanogan County).

Although it was not verified that such an annual cycle occurs every year, one piece of evidence favoring this interpretation can be offered. As will be recalled, an eighteenth sample of birds was collected in the winter of the following year. The results from these have been presented in table 2 where it is seen that the mean value of E% for these 10 birds is 74, which is in good agreement with the winter values of the previous year.

It can be mentioned at this point that no significant differences in E% were demonstrable between males and females or between first-year and adult birds. Hence, in the results just mentioned, as well as in the experimental results presented beyond, all four of these categories are included.

Correlation of thyroid activity with air temperature.—The shape of the curve of thyroid activity is remarkably similar to the general form of the annual cycle of air temperatures to which the birds were subject. This is readily apparent in figure 1 and has been confirmed by the following statistical test. For this test, E% values were read from the curve in figure 1 at the end of each half-month period and plotted against the mean temperature for that half-month, T (°C.). Half-month periods preceding the day to which E% values correspond were chosen because it is known that, under laboratory conditions, small birds take roughly half a month to adapt their metabolic rate fully to a new temperature (Gelineo, 1955). Evidence was also obtained in our own investigations that complete adaptation of thyroid activity of *Z. l. gambelii* to a new temperature could take place within less than half a month.

Upon plotting the data relating E% and T it appeared that the relation was linear. The straight line of best fit, calculated by the method of least squares is

$$E\% = 71.3 - 1.22\,T$$

The coefficient of correlation (r) between E% and T is relatively high; $r = -0.84$, after correction for the small number of points involved. The range of r encompassed by three standard errors, computed by means of the z-transformation (Waugh, 1943), is -0.51 to -0.96, which shows that the value of r is very significantly different from zero. The correlation between E% and the average temperature during the preceding half-month is, therefore, surprisingly close, in view of the large random errors to which the individual values of E% and T must each be subject. This suggests that the annual cycle of air temperatures may be the cause of the annual cycle of thyroid activity in these birds.

Experiments with temperature and day length.—If the annual cycle of thyroid activity in White-crowned Sparrows is due to air temperature, thyroid activity would be expected to change in response to artificial changes in air temperature. To test this, six birds that had been living in the outdoor aviaries in winter (average temperature 0°C., day length 8 hr.) were brought indoors (temperature 26°C., day length 8 hr.). The thyroid activity of these birds decreased from the prevailing winter level (mean E% >70) to a value typical of summer thyroids (mean E% = 47) in less than 7–11 days. Although it is possible that some overlooked indoor factor was responsible for this striking change in thyroid activity, it appears likely that the factor responsible was the temperature.

It was also thought in view of the foregoing that thyroid activity of this species should not change when other factors that are cyclic in the natural environment are

Table 3

Effect on Thyroid Activity (E%) of Treating Birds with Daily Photoperiods of Different Length

Experiment	Air temperature in degrees centigrade	Duration of experiment in days	Short photoperiods[1]		Long photoperiods[1]	
			Number of birds	Mean E%	Number of birds	Mean E%
1	26	0	....	....	6	47
		6	....	....	6	46
		12	....	....	6	51
		18	....	....	6	50
		24	....	....	6	55
		30	....	....	6	36
2	12	23–26[2]	4	42	4	42
3[3]	26	0	4	50	....	....
		10	5	53	5	49
		22	4	48	4	52

[1] Short photoperiods were 8 hours in experiments 1 and 3, and 9 hours in experiment 2. Long photoperiods were 18 hours in experiment 3 and 20 hours in experiments 1 and 2.

[2] In experiment 2 there was also an initial period of 6 days during which the photoperiod was progressively lengthened from 9 hours to 20 hours. This experiment was performed by Dr. J. R. King, who kindly allowed us to examine the thyroids of the birds (King and Farner, 1956).

[3] All birds used in this experiment were castrates.

artifically changed. The following experiments show that changes in day length have no effect on thyroid activity under the conditions employed. Birds that had been adapted in winter to room temperature (12°C. or 26°C.) and winter day lengths (8 hr.) were exposed to long day lengths (18 or 20 hr.). Table 3 summarizes several experiments of this sort. It shows that these birds did not change their thyroid activity appreciably in response to the long day lengths. Furthermore, because long day lengths induce many physiological changes in these birds, such as gonadal development, a light molt, and fat deposition, it can be concluded that none of these internal changes affect thyroid activity.

Included in table 3 are the results of an experiment performed with castrated birds. The birds were castrated at least a month before the beginning of the experiment to allow complete healing. After the experiment it was verified, by examination of serial sections of the areas normally occupied by the gonads, that castration had been complete. Castrated birds were used because of the possibility that sex hormones depress thyroid activity in birds (Benoit, 1950; Maqsood, 1952). It was possible, therefore, that any increase in thyroid activity that might tend to occur in response to long photoperiods would be checked in normal birds by sex hormones produced by the rapidly developing gonads. Nevertheless, as can be seen in table 3, E% was not affected by the photoperiodic treatment whether or not the birds were castrated.

DISCUSSION

The thyroid cycle of the race Z. l. gambelii.—The results of our investigation show that there is a striking annual cycle of thyroid activity in *Z. l. gambelii* of eastern Washington. In addition, two lines of evidence have been obtained which are consistent with the view that the cycle found is caused by the annual cycle of air temperature. The first line of evidence shows that thyroid activity in wild populations is closely correlated with the mean air temperature during the preceding half-month. Indeed the correlation may possibly be closer than the statistical test indicated because of errors not only in the values of E% but also in the values of temperature used. So it is perhaps worth pointing out some major errors to which the values of temperature used are subject. First, the actual average temperature for a half-month period is only approximately indicated by averaging the daily maxima and minima. Second, the average air temperature that the birds experienced was probably never quite the same as that at the weather station a few miles away. Third, it is unlikely that thyroid activity could be expected to reflect even the actual average temperature experienced during the preceding half-month. Rather, one would expect some average temperature weighted in favor of the preceding few days to be reflected.

The experimental results provide the second line of evidence consistent with the view that the thyroid cycle found is due to the annual cycle of temperature. In these experiments temperature appeared to affect thyroid activity strongly enough to account for the amplitude of the thyroid cycle in wild birds. But neither day length nor any of the physiological changes induced by long photoperiods affected thyroid activity detectably.

A further line of evidence in favor of this temperature hypothesis comes from comparing the results of our investigation with those of the recent extensive investigations of Oakeson and Lilley (1960) on the same race. These authors have studied thyroids from birds on wintering grounds in California (lat. 34°N) and on breeding grounds in Alaska (lat. 62–65°N). Their birds, in distinct contrast to ours, were found to show no great change in the monthly mean of thyroid activity, as measured through the course of the year by another histological index. The absence of a pronounced cycle of thyroid activity appears to be connected with the fact that the amplitude of the cycle of temperature their birds experienced was small, probably 5°C. Thus the monthly mean tem-

Table 4

Annual Cycles of Thyroid Activity of Passerine Species in Regions Where There Is a Pronounced Annual Cycle of Air Temperature[1]

Species	Period of the Year[2] Winter	Molt	Migration	Reproductive activity	Reference
Passer domesticus	X	O	....	O	Watzka, 1934
	O	X	....	X	Küchler, 1935
	X	X	....	O	Woitkewitsch and Nowikow, 1936
	X	O	....	O	Miller, 1939
	X	X	....	X	Gál, 1940
	O	X	....	....	Bigalke, 1956
Passer montanus	O	X	(X)	O	Küchler, 1935
	X	X	....	O	Woitkewitsch and Nowikow, 1936
	O	....	....	....	Gál, 1940
	(X)	O	....	X	Nakamura, 1958
Emberiza citrinella	O	X	(X)	O	Küchler, 1935
Zonotrichia leucophrys	X	O	O	O	present authors
Serinus serinus	X	X	....	O	Takewaki and Mori, 1944
Chloris chloris	O	X	(X)	X	Schildmacher, 1956
Fringilla coelebs	O	X	....	X	Bigalke, 1956
	....	....	X	X	Gál, 1940
	....	X	....	O	Vaugien, 1948
Pyrrhula pyrrhula	X	....	....	....	Gál, 1940
	O	....	....	....	Putzig, 1937
Loxia pytyopsittacus	O	....	....	....	Putzig, 1937
Loxia curvirostra	X	....	....	....	Putzig, 1937
Bombycilla garrulus	O	....	....	....	Putzig, 1937
Oriolus oriolus	....	....	X	....	Gál, 1940
Parus major	O	X	....	X	Bigalke, 1956
	O	X	....	O	Vaugien, 1948
Sylvia communis	O	....	....	....	Merkel, 1938
Muscicapa striata	....	....	....	X	Gál, 1940
Erithacus rubecula	O	X	X	O	Küchler, 1935
	O	....	....	....	Merkel, 1938
Turdus merula	O	X	....	X	Bigalke, 1956
Turdus viscivorus	X	....	....	....	Gál, 1940
Turdus pilaris	O	....	....	....	Gál, 1940
Turdus philomelos	....	....	X	....	Gál, 1940
Hirundo rustica	....	X	....	....	Gál, 1940
Sturnus vulgaris	O	....	....	X	Burger, 1938
	O	X	....	X	Bigalke, 1956
Garrulus glandarius	....	....	....	X	Gál, 1940
	O	....	....	....	Putzig, 1937
Pica pica	X	....	....	X	Gál, 1940
Corvus frugilegus	O	....	....	....	Gál, 1940
Corvus corone	O	....	....	X	Haecker, 1926
Instances of X	11	17	4	14	
Instances of O	22	4	1	11	

[1] A pronounced annual cycle of air temperature is defined, for present purposes, as one in which the mean temperature of the coldest winter month is at least 20°C. lower than the mean temperature of the hottest month of the year.

[2] Thyroid activity in each period is symbolized as follows: X or (X), high or intermediate at some time; O, low throughout; ...., no observation reported. Sometimes the reason no observations are reported for migration is that the species is not migratory, as in *Passer domesticus*.

peratures from October to April, on the wintering grounds, ranged between 12°C. and 17°C. From late May to August, on the breeding grounds, the mean temperatures also appear to have fallen within this same range. By contrast, in eastern Washington where our investigations were carried out, the amplitude of the annual cycle of monthly mean temperatures is much greater, namely 20°C. (0°C. to 20°C.). This, therefore, constitutes a third line of evidence that the pronounced cycle of thyroid activity encountered in our investigations is due to the pronounced cycle of temperature involved. Conversely, therefore, the lack of a pronounced cycle of thyroid activity encountered in the investigation of Oakeson and Lilley may be due to the lack of a pronounced cycle of temperature.

It should be noted that a second inference can tentatively be drawn from comparison of the results of the present investigation with those of Oakeson and Lilley (1960) on the same race of birds. Since the two groups of birds studied belong to the same race, they must be genetically similar. Yet one group exhibits a pronounced thyroid cycle whereas the other does not. As only the environments of the two groups are very different it seems that the thyroid cycle is more likely to have an environmental cause than an innate cause. This inference appears to stand regardless of whether we have been correct in suggesting that the external cause is temperature.

The thyroid cycles of other passerine birds.—Although our three lines of evidence give strong support to the hypothesis that air temperature is responsible for the main features of the annual cycle of thyroid activity in *Z. l. gambelii*, the majority of passerine species investigated do not appear to exhibit high thyroid activity in cold winters. In order to support this assertion, an attempt has been made to present (table 4), for the first time, a summary of observations made on thyroid activity of passerine species in regions where there are pronounced annual cycles in air temperature. A pronounced annual cycle of temperature is defined, for present purposes, as one in which the mean temperature of the coldest month is at least 20°C. colder than that of the hottest month of the year. The criteria for thyroid activity in the table are histological except in the case of Vaugien (1948) who used thyroid weights. In 12 of the 34 cases in which winter thyroids were examined, no observations were reported for other times of the year; in these cases the authors simply report that thyroids were active or inactive relative, presumably, to the thyroid activity of some other species in winter. In the remaining 22 cases, winter activity is relative to activity at some other time of the year. Even if consideration is restricted to these 22 cases, it is apparent that in the majority (13) of them thyroid activity is reported not to be high in winters that are 20°C., or more, colder than summers in the same region.

It might have been expected that thyroid activity of all birds should be higher in cold winters than in summer. For it is well known that warm adapted laboratory homeotherms raise their thyroid activity after a week or two in a cold environment (Hensel, 1955; Hart, 1958). Because of this the basal rate of energy metabolism rises thereby helping the animals to maintain their normal body temperature in the cold environment. Hence the many instances of birds that do not show histological signs of high thyroid activity in cold winters requires explanation.

One possible explanation is that the role of the thyroid in mediating the rise in basal metabolic rate in response to cold is not important in these cases. Experimental evidence obtained with rodents suggests that the thyroid need not have an essential role in this response (Hart, 1958). This opens the possibility that the relative role of the thyroid in adjusting the basal metabolic rate to cold may differ in different species.

Another possible explanation, as Dr. Oakeson reminded us, is that other mechanisms of adapting to cold may be used by some species to the virtual exclusion of the mechanism involving basal metabolic rate. Insulative mechanisms, increased muscular activity (Scholander *et al.*, 1950; Hart, 1958) and, in extremes of cold, lowered body temperature (Steen, 1958) are all instances of such mechanisms found to operate in small birds.

A third possible explanation of the failure of many birds to exhibit elevated thyroid activity in cold winters might be that in these birds thyroid activity is not reflected histologically. Until recently a close correlation between the results of radioactive and histological methods of measuring thyroid activity had been observed in laboratory homeotherms. Recently it was suggested that hamsters may be an exception to this rule (Knigge, 1957). However, it appears that Knigge's interpretation may not preclude the possibility that his results were due to an influence of light. Light has been shown to affect thyroid activity of other rodents (Puntriano and Meites, 1951; Soliman, Badawi, and Ghanem, 1958). Nevertheless, even if hamsters are not a real exception, the possibility remains that some of the passerine species evincing no histological signs of high thyroid activity in cold winters are exceptions. That is to say, these species might be found by radioactive methods to have high thyroid activity in cold winters.

As is apparent also in table 4, many investigators have reported that thyroid activity is relatively high at periods of the year other than winter. Commonest are the periods of molt, reproductive activity (that is, gonadal development or breeding), and migration. However, careful examination of our data gives no evidence that thyroid activity is elevated in any of these periods in *Z. l. gambelii.* Comparable results were obtained by Watzka (1934) and Miller (1939) with *Passer domesticus.* Miller's results were obtained by measurements of metabolic rate as well as by histological methods.

Again, it is difficult to reconcile the differences in the results of different investigators. If the results are accepted as providing valid pictures of the annual cycles of thyroid activity in passerine birds, then it follows that different species in similar climates must differ enormously in the form of these cycles. Indeed, if this explanation is accepted, populations of *Passer domesticus,* in different geographic areas of the northern part of the north temperate zone, must also differ enormously in their annual cycles of thyroid activity (table 4). However, it should be recalled that the experimental evidence that molt (Höhn, 1950), reproductive activity (Benoit, 1950; Maqsood, 1952), or migration (Farner, 1955) are naturally dependent on especially enhanced thyroid activity has never been more than suggestive. Even the best supported case, that of molt, has now been questioned because of recent experiments on the domestic fowl (Shaffner, 1954; Tanabe, Himeno, and Nozaki, 1957; Juhn and Harris, 1958).

It is evident that much remains to be done before a satisfactory understanding of the forms and causes of the annual thyroid cycles in passerine birds, as a group, can emerge.

SUMMARY

A description of the annual cycle of thyroid activity in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) of eastern Washington has been given. Thyroid activity, measured by a histological method, is high in autumn and winter, intermediate in spring, and low in summer.

The populations of the same race studied by Oakeson and Lilley (1960) elsewhere do not exhibit such a cycle. This suggests that the cycle exhibited by *Z. l. gambelii* in eastern Washington is caused by an environmental factor. Three lines of evidence suggest that this external factor is air temperature: (1) Thyroid activity of wild populations of *Z. l. gambelii* in eastern Washington was found to be closely correlated with the mean temperature of the preceding half-month. (2) Experiments showed that tem-

perature had an effect on thyroid activity of captive *Z. l. gambelii* sufficient in magnitude and direction to account for the cycle observed in nature. (3) The environment of the populations without a pronounced thyroid cycle differs most obviously from the environment in eastern Washington by the absence of a pronounced cycle of temperature.

Attention is drawn to the fact that the majority of passerine birds hitherto investigated do not give histological evidence of high thyroid activity in cold winters. Attention is also drawn to the great variation, among reports on various passerine species, concerning possible roles of thyroid activity during molt, reproductive activity, and migration.

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