THE ROLE OF THE PITUITARY, FAT DEPOSITION, AND BODY WEIGHT IN BIRD MIGRATION

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INTRODUCTION

Beginning in 1937 a series of studies was undertaken to determine the regulative factors involved in the annual stimulus for bird migration. The most promising theory concerning regulation which had appeared in recent years was that of Rowan (1929, 1932) which postulated direct control by gonadial secretions. Some aspects of the theory were based on experimental work and perhaps because of this his ideas were fairly well received by most biologists. Almost ten years elapsed before further experiments were designed to test this theory, and the results of these experiments were not corroborative. Instead, the new facts which were ascertained necessitated the formulation of another explanation which stressed the total physiological and psychological condition of the bird (Wolfson, 1940).

These later experiments, which had to do with delayed migration, led to still others designed to induce migration out of season. From them conclusive evidence was obtained for the first time to prove that a northward migration in mid-winter could be induced among winter residents by artificial means. In addition to the experiments, studies were made of the gonads and their role in migration (Wolfson, 1940, 1941, 1942). The problem of determining the mechanism whereby external factors effect physiological changes within the bird also was considered. The evidence in support of current theories was evaluated and reinterpreted from the point of view of our modern knowledge of the functions of the hypothalamus (Wolfson, 1941).

The purpose of the present paper is, first, to describe additional experiments, second, to present data which lead to an understanding of the role of the pituitary, fat deposition, and body weight in regulating migration, and third, to summarize the results of all the studies in the series and to restate the conclusions in the light of all the data now available.

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EXPERIMENTAL PREVENTION OF MIGRATION

Results and conclusions of earlier, related experiments.—The results of the experiments in delayed migration had shown that Oregon Juncos (*J. oreganus thurberi, J. o. shufeldti, J. o. montanus, J. o. oreganus*; nomenclature from Miller, 1941) which winter at Berkeley, California, and breed as far north as Yakutat Bay, Alaska, would migrate two months later than usual even though their gonads were in breeding condition. The experiments in induced migration showed that juncos could be induced to migrate two months earlier than usual by subjecting them to artificial increases in day length. In the former case, migration occurred in early June, in the latter case in late January. Normally, migration occurs in late March and early April. The factors involved in producing these results were classified as external (environmental) and internal (physiological).

The external factors of day length and temperature to which these two groups of birds had been subjected before migration and the condition of these factors during the time of migration were not identical. In the delayed migration experiments the juncos were held in outdoor aviaries until June and consequently were subjected to the natural changes in day length and temperature. In the induced migration experiments the day lengths were increased artificially by means of light bulbs from December 10 to the end of January. The total day length on the date of release was approximately the same for both groups. The rate of increase and the length of day during migration were, therefore, markedly different for each group. The single feature of the environment which was similar for both groups was that prior to the time of migration the day lengths were increasing. It was concluded, therefore, that the primary external stimulus for the spring migration was the daily increases in day length.

Among internal factors, the recrudescing gonads, in the male particularly, have been considered as a stimulus for migration. In these two groups, the gonads were in completely different stages. In the June group the testes, with a combined volume of 250 mm.^{3}, were in breeding condition at the time of release and were in no way different from the testes of males already on their breeding grounds far to the north. In the January group the testes, with a combined volume of 5-10 mm.^{3}, were in a stage similar to that which occurs at the normal time of migration and were only 4 per cent of the size of the June group. It seemed, therefore, that a particular state of the testes was not required as a stimulus for migration. An internal factor which was found to be correlated with migration was a deposition of fat and the accompanying increase in body weight. The fat was most conspicuous subcutaneously along the pterylae, in the furculum, in the uropygial and abdominal regions, and intraperitoneally. Four classes were designated to indicate the degree of fat deposition: none, little, medium and heavy. In both the January and June groups most of the birds had a heavy deposition of fat at the time of release, and only those individuals which did not have this heavy fat deposition failed to migrate and were recaptured. It was concluded, therefore, that a heavy deposition of fat, a readily discernible internal factor, and the concomitant increase in weight, were a fundamental part of the internal situation necessary for migration.

Since this change in body weight occurred prior to the northward migration and under day-length conditions which were alike only in that they were increasing, the question arose as to whether a similar change in body weight occurs preceding the fall migration when the day lengths are decreasing. In addition, there were other relevent problems. Would this fat be utilized if the spring migration was prevented? If breeding was prevented would the gonadial changes in individuals retained at Berkeley be comparable to those of individuals on their breeding grounds? In an attempt to solve these problems an experiment was performed in which the spring migration was prevented.

Experiment 7.—A small group of migrant juncos trapped in February and March was not included in the June release of 1939 but was retained until October. It was planned to sample the birds regularly through the summer, but due to a high mortality only eight birds were available and the plan could not be instituted. Instead, two groups of samples were taken, one on August 9 and one on October 1. In addition, the birds were examined on several occasions, and one group was sampled at the start of the experiment. All the samples which were taken are recorded in table 1.

Table 1

Samples taken in prevention of migration experiment, 1939

Date	Sample No.	Sex	Race	Testis size mm.	Testis volume, mm.^{3}	Body weight, gm.	Fat class
June 7	90	♀	S			18.1	Heavy
June 7	91	♂	S	L—7.6×6.1 R—6.8×6.1	147.95 130.79	17.6	Heavy
June 7	92	♂	S	L—7.1×5.6 R—6.9×6.7	116.50 161.77	15.4	Little
Aug. 9	101	♂	T	L—1.2×1.0 R—..........	.65	15.3	None
Aug. 9	102	♂	T	L—1.6×1.1 R—1.6×1.1	1.01 1.01	16.2	None
Aug. 9	103	♂	S	L—2.6×2.1 R—2.7×1.9	6.00 5.09	16.1	None
Oct. 1	109	♂	T	L—1.2×.9 R— .9×.9	.40 .38	18.1	Heavy
Oct. 1	110	♀	S			20.4	Heavy +
Oct. 1	111	♂	T	L—1.2×.8 R—1.2×.9	.40 .51	16.9	Medium
Oct. 1	112	♀	S			17.0	Medium+

Examination of the birds revealed that the annual molt was begun early in July. At this time the birds showed only a slight amount of fat, in contrast to the heavy deposition of fat which they had at the beginning of June. Under natural conditions the annual molt begins in late July and August. On August 9, three samples were taken, two male *thurberi* and a male *shufeldti*. The birds had completed about half of the molt. In two of them all the rectrices were only half grown. The testes had regressed to an average combined volume of 4.5 mm.^{3}, and histologic examination revealed that the cells within the tubule, except a single row of spermatogonia, were degenerating. The samples did not have any fat. The five remaining birds were similar to the samples in stage of molt and in fat condition.

On September 5 examination of the birds showed that the molt was almost completed. One bird had a heavy deposition of fat, two a medium amount, and two a small amount. On October 1, four samples were taken, two male *thurberi* and two female *shufeldti*. The fat class in one of the birds of each sex was heavy, and it was medium in the others. The gonads had completely regressed and were at winter minimum. All the birds had completed the molt. Wild migrants which had arrived in Berkeley in October showed no fat, and the gonads were at winter minimum.

One bird, a female *montanus*, was not sampled. It was released in experiment 6 on June 8, 1940, at which time it showed a heavy deposition of fat. It is noteworthy to trace the history of this bird. It was caught in late March in 1939 and placed in the outdoor cages. At the time of capture its fat condition was not determined, but judging from other individuals it probably reached a heavy fat condition before June. When it was examined for the first time early in July, it showed no fat and was molting. By September 5 the molt was practically completed, and the bird had a heavy deposition of fat. On October 1, its fat condition was unchanged. It was retained in the outdoor cages until June 8, 1940, when it showed a heavy deposition of fat and was released in Experiment 5. Since it was not retrapped, it is assumed that it migrated with the other individuals in the experiment.

These observations show that although the juncos were on their wintering grounds in the summer, they molted, their gonads regressed, and they became progressively fatter as the time for the fall migration arrived. There can be no doubt that similar changes occur in wild juncos on their breeding grounds after the completion of the breeding cycle. It is concluded, therefore, that the inhibition of two phases in the annual cycle—the northward migration and breeding—and the retention on the wintering grounds did not prevent the occurrence of the normal, subsequent phases of gonadial regression, molt, and "preparation" for the fall migration, as manifested by the heavy deposition of fat.

LIGHTING EXPERIMENTS IN THE FALL

Experiment 8.—Riley (1936) reported that in the English Sparrow, immature individuals responded readily to increases in illumination in October, whereas adults that had bred failed to do so until November. Bissonnette (1937) postulated that birds migrate in the fall due to the regression of pituitary activity and do not breed on the wintering grounds because this gland and hence the gonads remain in the "refractory phase." Blanchard (1941), although she performed no experiments with White-crowned Sparrows, asserts (pp. 76-77): "We are faced, then, with the fact of a gonad cycle which cannot be initiated by any external factor . . . . The environment may be thought of as responsible for variations in the rate and duration of early testis development but only within certain limits set by the hereditary clock-work of the population."

The purpose of experiment 8 was to determine whether gonadial recrudescence could be induced in the fall in the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli, Z. l. pugetensis, Z. l. gambelii*) and the Oregon Junco and thereby to gain evidence for the support or refutation of Blanchard's and Bissonnette's conclusions. The birds were trapped in August, September, and October, 1940, and at the start of the experiment on October 18, 21 White-crowned Sparrows and 11 Oregon Juncos were available. The normal day length for October 18 is 11 hours and 7 minutes. An initial increase was made of 1 hour and 8 minutes, making a total day length of 12 hours and 15 minutes. Thereafter, the average daily increase was 7.5 minutes until a day length of 15 hours was reached on November 19. That day length was maintained until the termination of the experiment on December 1.

The first samples of Oregon Juncos were taken on November 11, and none of the birds showed any gonadial response. Included in the group of samples were 4 immature male *pinosus*, 2 immature female *pinosus*, and 1 adult male *thurberi* (*pinosus* is a non-migratory race of the Oregon Junco). The next sample was an immature male *pinosus* taken on November 19. It also showed no gonadial response. On December 1, an adult male *shufeldti*, an immature female *thurberi*, and an immature female *pinosus* were sampled. After 6 weeks of treatment there was still no gonadial response, and none of the migrant samples showed a deposition of fat. Table 2 summarizes the data obtained from the samples and includes wild controls which were collected at the start and after the completion of the experiment.

Samples of White-crowned Sparrows were taken on November 11, 19, 30 and December 1, and they showed a definite response to the experimental treatment. It is planned to publish the results in detail at a later date along with other data for this species, but at this time some definite observations may be presented. The response comprised the recrudescence of the gonads, the assumption of a heavy amount of fat in the migrants, and the induction of the prenuptial molt—all of which events occur normally in this species preceding the spring migration early in April. Particularly striking was the molt in the crown of a few immature birds, where it had progressed almost to the middle of the crown by the end of the experiment. The resident *Z. l. nuttalli* and the migratory *Z. l. pugetensis* showed differences in gonadial recrudescence and assumption of fat comparable to those which occur under natural conditions, as described by Blanchard (1941), and comparable to those which occurred in resident and migrant juncos under experimental conditions in the winter (Wolfson, 1942).

The lack of any response in the juncos (3 adults and 8 immatures) indicates that a refractory period in the response of the pituitary to increasing day lengths exists in the fall, at least in the immature residents. More data must be available before it can be asserted that a refractory period occurs in the adult residents or migrants. Since the migrants do not arrive in good numbers until November, it would be difficult to obtain conclusive evidence in Berkeley for the solution of this problem. Evidence from a summer resident species which could be trapped on the breeding grounds in August and September and subjected to lighting experiments would be more conclusive.

Table 2

Samples taken in lighting experiment in the fall of 1940

Date	Sample No.	Sex	Race	Testis size, mm.	Testis volume, mm.^{3}	Body weight, gm.	Fat class
Oct. 16	234	♂	S	L—1.4×1.1 R—1.4×.9	.89 .59	18.5	None*
Oct. 21	237	♂ im.	P	L— .9×.6	.17	14.0	None*
Oct. 21	238	♂ im.	P	L—1.1×.6 R— .9×.8	.21 .30	14.7	None*
Oct. 22	241	♂	O	L—1.2×1.0 R—1.1×1.0	.65 .58	17.8	None*
Nov. 11	247	♂	T	L—1.2×1.0 R—1.2×1.0	.65 .65	15.2	None
Nov. 11	248	♂ im.	P	L— .9×.6 R— .8×.6	.17 .15	15.0	None
Nov. 11	249	♂ im.	P	L—1.0×.6 R— .9×.8	.19 .30	16.0	Little
Nov. 11	250	♂ im.	P	L—1.0×.6 R— .9×.8	.19 .30	16.1	None
Nov. 11	251	♂ im.	P	L—1.0×.7 R—1.0×.7	.26 .26	16.3	None
Nov. 11	252	♀ im.	P			16.0	None
Nov. 11	253	♀ im.	P			16.0	None
Nov. 19	254	♂ im.	P	L—1.2×.9 R—1.0×.9	.51 .42	15.8	None
Dec. 1	257	♂	S	L—1.0×.7 R—1.0×.7	.26 .26	15.1	None
Dec. 1	258	♀ im.	T			12.8	None**
Dec. 1	259	♀	P			11.5	None**
Dec. 5	261	♂ im.	T	L—1.0×.7 R—1.0×.8	.26 .34	18.9	None*
Dec. 5	262	♂ im.	P	L—1.0×.8 R— .9×.9	.34 .38	20.0	None*

* Indicates wild controls sampled at beginning and end of experiment.
** These two birds had been dead for several hours before they were discovered and examined.

The reaction in the White-crowned Sparrows indicates that there is no refractory period in the response of the pituitary in the fall. Moreover, the fact that this species responded to the increases in day length and the fact that residents and migrants responded differently under identical experimental conditions of day length would seem to me to invalidate Blanchard's assertions regarding the role of the external environment in the initiation and subsequent course of the gonadial cycle.

Experiment 9.—To gain further evidence for the view that increases in day length can induce gonadial recrudescence in the White-crowned Sparrow, and to substantiate the differential response of the residents and the migrants, the experiment of 1940 was repeated in 1941. Sixty individuals were available at the start on November 6, but the experiment was terminated on December 11 with the outbreak of the war. The initial increase in day length was one hour and 5 minutes, making a total day length of 11 hours and 32 minutes. An average daily increase of 7.5 minutes was continued until December 11, when the day length was 15 hours and 15 minutes. Due to the sudden termination of the experiment, the birds were sampled as rapidly as possible, and by December 18 most of them had been examined and preserved.

The results confirmed the previous observations that increase in day length could induce gonadial recrudescence, prenuptial molt, and deposition of fat in the migrants; in addition, the differential response in the residents and the migrants was again demonstrated.

There were included in this experiment a few individuals of other species, and they all showed a good gonadial response. The species represented were the Golden-crowned Sparrow (*Zonotrichia coronata*), the Song Sparrow (*Melospiza melodia*) and the Fox Sparrow (*Passerella iliaca*).

THE ROLE OF THE PITUITARY

The results of the experiments in migration indicated that the gonads and the sex hormones were not the primary stimulus for the initiation of migration. Rather, the results required the postulation of a more general internal stimulus of which the recrudescing gonad and the heavy deposition of fat were merely two manifestations. The fact that the development of the gonad is controlled by the pituitary and that a change in body metabolism which would yield a heavy deposition of fat could be produced by the endocrine system indicated that the pituitary was the governing organ in the production of the internal stimulus. Our modern knowledge of the functioning of the pituitary presents no grounds for doubting this contention. Yet it seemed highly advisable to obtain direct evidence in the Oregon Junco. Two types of studies were undertaken—experiments involving the administration of pituitary and pituitary-like hormones, and a cytological study of the anterior lobe of the pituitary.

The experiments were designed, first, to determine whether the increase in the size of the gonad and the secretion of the bird's own sex hormones resulting from injections of gonadotropic hormones would alter the metabolism of the bird to the extent of inducing fat deposition, and second, to determine whether the manifestations of the internal stimulus for migration (recrudescing gonads and a heavy deposition of fat) could be induced by the administration of anterior pituitary extracts or other hormones.

The cytological study was undertaken to determine whether visible evidence of an increase in the activity of the pituitary could be correlated with the change in the physiological state of the bird which precedes migration and which can be produced out of season by means of artificial light. Moreover, if it could be demonstrated that the pituitaries of the resident and migrant Oregon Juncos responded differently to the same experimental conditions of day length, this would be prima-facie evidence of the inherent difference in the response of the endocrine system to identical features in the external environment and would strengthen the view that external factors, and not automatic internal rhythm, play a primary role in regulating the time of breeding and of migration.

ADMINISTRATION OF HORMONES

Experiment 10.—The first experiment was performed in January, 1942. Oregon Juncos were trapped in December and brought into the laboratory where they were housed for the duration of the experiment. They were subjected to normal day-length conditions. The room which contained the cage was small; it had no source of heat, and the windows occupied the north wall almost completely. The windows were open at all times, and the temperature indoors was equivalent to that out of doors. The birds were fed unmixed Argentine canary seed and food and water were available at all times.

The purpose of this experiment was to determine the gonadial response and fat deposition in residents and migrants when injected with the same doses of gonadotropic substance.

Twenty-nine birds were available at the beginning of the experiment on January 2. Four of these were used as controls and were injected with physiological saline; the remainder were injected intramuscularly with 0.1 cc. (5 rat units) of pregnant mare serum (Gonadin Serum, Cutter Laboratories). Seventeen injections were administered in nineteen days. Included in the experimental group were 12 residents (8 males and 4 females), and 13 migrants (11 males and 2 females). In this report only the gross results will be given.

The females (4 *pinosus*, 1 *thurberi*, and 1 *shufeldti*) showed a slight ovarian response, whereas the males (8 *pinosus*, 5 *thurberi*, 2 *shufeldti*, 2 *oreganus*, and 1 *J. h. hyemalis*) showed a good gonadial response. The resident and migrant males showed no significant difference in their gonadial response, and there was no deposition of fat. Under natural conditions, fat deposition accompanies the recrudescence of the gonads in the migrants.

The lack of any fat deposition would seem to indicate that the sex hormones which are produced by the developing gonad can not induce, nor can they be the controlling factor for, the deposition of fat. The fact that the resident and migrant males did not differ in the amount of gonadial response demonstrates that the normal differences in their gonadial cycles are not due probably to differences inherent in the testis, but rather they are due to a difference in the activity of the pituitary. The slight response of the ovary is in agreement with its response in the increased day-length experiments.

Experiment 11.—The second experiment of this series was performed in March of the same year. Had the birds been available, the experiment would have been started sooner, for by this date the testes had already begun to recrudesce. This experiment was designed as an exploratory one and the results are offered in the nature of a preliminary report. The purpose was to ascertain which anterior pituitary hormones could be administered, and in what doses, to obtain a response such as that which occurred in the migrants in the induced migration experiments. Included in this experiment were seven groups of experimental birds in addition to the controls. The control group included 7 females (4 *pinosus*, 2 *thurberi*, and 1 *montanus*) and 5 males (2 *pinosus*, 2 *thurberi* and 1 *shufeldti*). Eleven injections were administered intramuscularly, one a day, in the period from March 3 to March 16. The hormones injected in each group and the results are summarized below.

Group 1. Four birds, 2 males (1 *oreganus* and 1 *thurberi*) and 2 females (*oreganus*) received 0.3 cc. (4.5 synergy rat units) of Synapoidin (chorionic gonadotropin plus follicle stimulating hormone from the anterior pituitary, Parke-Davis). The gonadial response was small in both males and females. There was no deposition of fat.

Group 2. Three birds, 1 male (*thurberi*) and 2 females (*thurberi*), received daily 0.3 cc. of Synapoidin plus ½ minim of adrenalin, 1/1000 dilution (Parke-Davis). There was no difference in the gross response of this group from that in group 1.

Group 3. Three birds, 2 males (1 *shufeldti* and 1 *montanus*) and 1 female (*shufeldti*) received daily 0.3 cc. (3 rat units) of Antuitrin G (growth hormone of pituitary primarily, plus small amounts of thyrotropic, gonadotropic and other hormones, Parke-Davis). They showed a heavy deposition of fat and an increase in gonadial size over the controls.

Group 4. Three birds, 2 males (1 *pinosus* and 1 *shufeldti*) and 1 female (*thurberi*), received 0.3 cc. Antuitrin G plus ½ minim adrenalin daily. The response of the gonads was essentially similar to that in group 3, but there was no deposition of fat. The pectoral muscles at the site of injection were badly discolored and edematous. This was also true in group 2 (Synapoidin plus adrenalin).

Group 5. Three males (1 *pinosus*, 1 *shufeldti*, and 1 *oreganus*) were given ½ minim of adrenalin alone. They all died within fifteen minutes after the injection. This observation is noteworthy since in groups 2 and 4 when Synapoidin or Antuitrin G was injected at the same time as the adrenalin, the same dose of adrenalin did not kill the birds.

Group 6. Four birds, 1 male (*shufeldti*) and 3 females (2 *pinosus* and 1 *shufeldti*) received 0.3 mg. of lactogenic hormone daily (prepared by Dr. W. R. Lyons of the Department of Anatomy, University of California). The gonads showed no increase in size over the controls, and there was a medium deposition of fat in the migrants.

Group 7. Four females were injected with higher doses of pregnant mare serum than were administered in the first group. Three (1 *pinosus* and 2 *oreganus*) received 50 rat units daily, and one (*thurberi*) received 100 rat units daily. The ovarian response of the females which received the lower dosage was only slightly in excess of the response of the females in group 1. The response of the female which received 100 rat units daily stood out in marked contrast to the response of the other females in this group, as well as in other groups. The ovary was much enlarged, and the oviduct had developed markedly. This strong response was no doubt due to the high dose which was administered. This female showed only a small amount of fat; the others in the group showed little or no fat.

Because of the small numbers of birds involved in each group, it is impossible to formulate at this time any definite conclusions with regard to the specific effect of each hormone. Nevertheless, there can be no doubt that the gonads of the juncos responded to the hormones of the anterior lobe, particularly the growth hormone, and also the pregnant mare serum. The results indicate that high doses are necessary to obtain a good response, especially in the females.

Of all the substances injected, only the Antuitrin G (growth hormone plus small amounts of other hormones) produced a reaction similar to that which occurred in the lighting experiments. Thus, judging from the gonadial response and the deposition of fat it would seem that by injections of Antuitrin G one could induce a pre-migratory physiological state. Whether birds so treated would migrate upon release remains to be determined by future experiments. It also remains to be determined whether birds treated in December and January would respond similarly to the birds in the above experiment which were treated in March.

The significance of the fat deposition in the juncos treated with Antuitrin G is emphasized by the fact that the birds treated with pregnant mare serum in experiment 10 showed a similar gonadial response, and yet no deposition of fat.

The injection of birds with adrenalin in this experiment was suggested by the results of Perry's studies on the role of adrenalin in the reproductive cycle of birds. Perry (1941*a*) had reported that adrenalin is antagonistic to the gonadotropic hormone in the English Sparrow. He performed a series of experiments bearing on the effect of adrenalin on the gonads. These included injections of Antuitrin G and adrenalin on alternate days, the injection of Antuitrin G alone, the injection of adrenalin into birds with advanced gonads brought about by increases in illumination, and the injection of adrenalin into wild birds with their gonads in breeding condition. The results of his experiments were uniform in their demonstration of the fact that when adrenalin was injected a regression of the gonads ensued, and conversely, adrenalin inhibited the gonadial response to Antuitrin G and to increases in illumination.

My observations, although few, are consistent, and demonstrate that a dose of ½ minim of a 1:1000 solution of adrenalin chloride (such as Perry used) is fatal to juncos when injected alone.

Lyman (1942) has criticized Perry's experiments, claiming that the dose used by

Perry was pathological and not physiological, and further, that the effect of injected adrenalin as an antagonist to the gonadotropic hormone is difficult to explain in view of its transient existence in the blood stream. The basis for these criticisms are the results of Lyman's experiments in which he repeated some of Perry's work. Using young pigeons he obtained only a moderate inhibition of the response of the gonads to gonadotropic hormone and a decrease in body weight. When a toxic substance, Witte's peptone, was substituted for the adrenalin, a similar decrease in body weight and moderate inhibition of the testes occurred. Lyman concluded that toxic substance injected in sublethal doses, as was the adrenalin, render birds incapable of responding normally because of their general detrimental effect on the health of the bird.

Although I am inclined to agree with Lyman, the results described by Perry cannot be dismissed so easily. We are at times too prone on the one hand to neglect physiological differences among species, and on the other hand to attempt to apply generally conclusions derived from one species or even one subspecies. Admittedly, generalizations are worth striving for if they are based on enough evidence, but at the same time the occurrence of a phenomenon in one population of a species and the explanation of that phenomenon for that population forms a part of the only foundation upon which generalizations can be built. Perry's results are difficult to interpret in the light of our present knowledge, but with additional evidence from studies on other forms we will be in a better position to interpret the data. In this regard, Perry (1941*b*) has experimented with rats and found that the response of the testes of the rat to experimental hyperadrenalism was not comparable with that which he found in the English Sparrow.

CYTOLOGICAL STUDY OF THE ANTERIOR LOBE OF THE PITUITARY

The specific structures of a glandular cell which give some indication of its secretory activity are (1) the granules which may be the precursors of the secretory product, (2) the Golgi apparatus, and (3) the mitochondria. Of these, the most reliable criterion of the functional state of the cell is the condition of the Golgi apparatus and consequently it was chosen for study in juncos.

That the Golgi apparatus is a reliable criterion has been shown by the numerous cytological studies of Severinghaus (1933, 1937), Koneff (1939), Reese, Koneff and Akimoto (1939) and other authors on the anterior pituitary. Also, Kirkman and Severinghaus (1938) in their recent and comprehensive review of the Golgi apparatus point out that the current concensus of opinion maintains that the Golgi apparatus is intimately concerned in the processes of secretion, and further, that the increase in cellular metabolism which is known to occur during secretion acquires additional cytological interest when correlated with the undeniable hypertrophy of the Golgi apparatus during the building up of the secretory product in the cell. Bourne (1942) in a more recent survey emphasizes again the role of the Golgi apparatus in the metabolism of the cell, particularly in the synthesis of substances within the cell, and he refers to recent studies on the relation between vitamin C and the Golgi apparatus as well.

To demonstrate the Golgi apparatus the Kolatchev method as modified by Nassonov was used (Severinghaus, 1932). The glands were imbedded in paraffin and sectioned at 4 micra.

Anterior pituitary in juncos with testes at winter minimum.—The condition of the Golgi apparatus when the testes are at winter minimum indicates that with regard to the secretory cycle most of the cells are in an "inactive" state. The Golgi appears as a compact, somewhat spherical or elliptical network embedded in the cytoplasm and closely associated with the nucleus. The meshes of the network are very small when they are visible, with the result that the usual appearance of the Golgi is that of a solid structure which is typically smaller than the nucleus. The cells are also small in size and the characteristic position of the apparatus is in the cytoplasm, yet touching the nuclear membrane. In those cells which contain but a narrow rim of cytoplasm, it may become flattened against the nucleus, depending upon the size of the cell. In figure 13, the four cells in the column at the left illustrate the condition of the Golgi apparatus which has been described. Selected fields from pituitaries of this type have been photographed and are shown in figures 14 and 15.

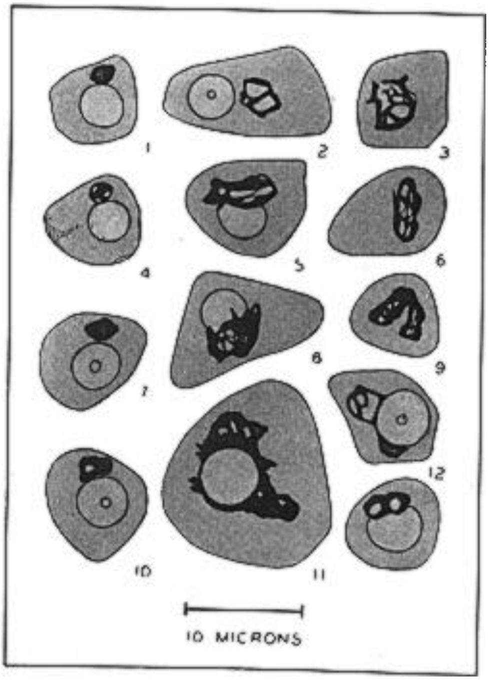

Fig. 13. Camera lucida drawings of cells from anterior lobe of pituitary of juncos illustrating condition of Golgi apparatus. The Golgi is indicated by thick black lines; nucleus circular with gray interior, sometimes containing a nucleolus. Cells 1, 4, 7 and 10 from wild migrant with testes at winter minimum; no. 270, January 3. Other cells from captive residents subjected to increases in day length whose testes were approaching breeding condition (stage 4, Wolfson, 1942): nos. 5 and 12 from no. 309, January 18; remaining cells from no. 307, same date.

The testes at this time show the following features: size of tubules at minimum; each tubule contains well defined row of uniform spermatogonia applied to basement membrane; cells between tubules predominantly connective tissue cells with some interstitial cells. The interstitial cells, however, do not resemble the more active phase of these cells that is present later.

Anterior pituitary in juncos with testes at breeding size.—The condition of the Golgi apparatus in these pituitaries stands out in marked contrast to those described above. The apparatus has hypertrophied to the extent that it may be two or three times its original size and equal to or larger than the nucleus. In addition to this general increase in size, another diagnostic feature of this state of the Golgi is the increase in the size of the meshes, producing an unmistakable "wide-mesh" network. The strands of the network (externum) blacken when the glands are treated with osmic acid and are therefore known as osmiophilic. The central region (internum) does not blacken and is termed osmiophobic. The close relationship with the nucleus remains basically unchanged, but as a result of the hypertrophy, part of the apparatus may extend on to the nucleus and in some cases completely surround it. The cells also show an increase in size. The fea-

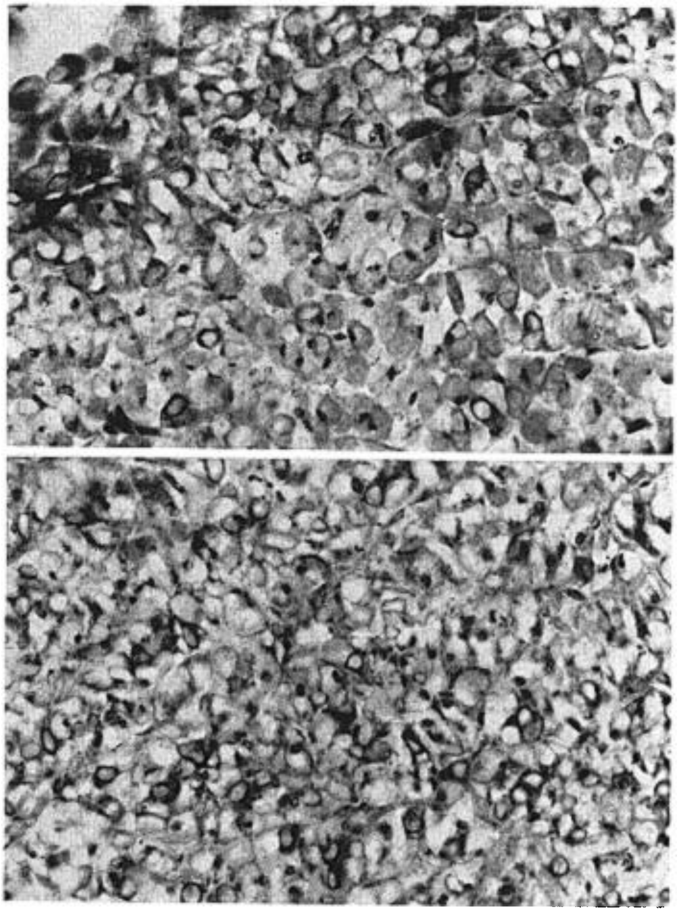

Fig. 14. Selected fields under low power from anterior lobe of pituitary of juncos. Upper, from captive resident with testes in breeding condition; no. 366, May 20. Note the large, heavily granulated cells. Lower, from wild resident with testes at winter minimum; no. 237, October 21. Note the smaller size of the cells. Photographs were taken with 1.4 oil immersion objective; magnification 1120 (reduced ½); Nassonov-Kolatschev preparations.

tures which have been described are shown in the drawings in figure 13, and in the photographs of selected fields in figures 14, 15, and 16.

Anterior pituitary in juncos with recrudescing gonads.—The minimum size of the testes, a combined volume of 0.5 mm.^{3} (stage 1 of Wolfson), is reached in the residents in late October, and the testes remain at this size through November and early December. Beginning in the middle of December there is a slight, gradual increase in size reaching a volume of 1.1 mm.^{3} by the middle of January. From this time until the end of March and early April when the testes reach their maximum size of 225 mm.^{3} there is a rapid increase in the rate of growth.

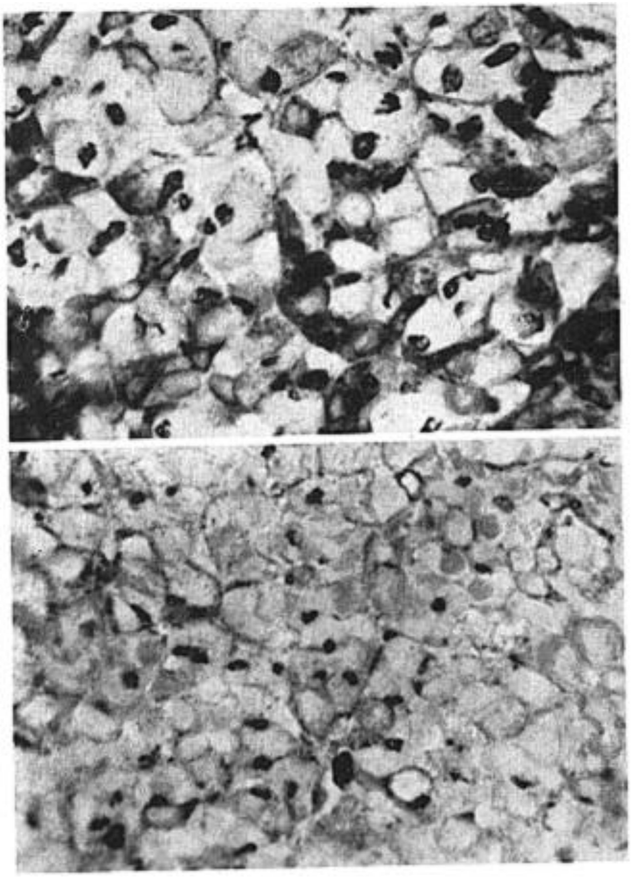

Fig. 15. Selected fields under high power to illustrate Golgi apparatus in "active" and "inactive" cells. Upper, from no. 307, from which drawings in figure 13 were made; shows enlarged Golgi with large meshes. Lower, no. 270, from which drawings were made, shows small, compact type of Golgi. Photographs taken with 1.4 oil immersion objective; magnification 1850 (reduced ½); Nassonov-Kolatschev preparations.

When the migrants arrive at Berkeley in October their testes are at the minimum combined volume of 0.5 mm.^{3} Through November, December, January and early February they increase only slightly to attain an average of 1.0 mm.^{3} on February 10. From this date until the end of March and early April, when migration begins, the testes attain an average volume of only 4.5 mm.^{3}—only a 9-fold increase over the winter minimum compared with a 550-fold increase in the residents in the same time.

Among the migrants, the Golgi apparatus in the pituitary cells does not show any marked development during the early stages of recrudescence, and it is not always possible to distinguish the pituitaries of these individuals from those with testes at the minimum size. By the time migration begins, the condition of the Golgi apparatus is more intermediate between the "inactive" and "active" states which have been described. These intermediate glands can be identified accurately, even though the cells exhibit more variability than occurs in the cells of either the "active" or "inactive" gland. No material was available for migrants with testes beyond the stage which occurs at the start of migration.

In resident birds with recrudescing gonads, the character and nature of the Golgi apparatus is no different from that in the migrants, but the time of occurrence of the types of Golgi apparatus is entirely different. At the end of March when the resident males are breeding, most of the cells in the anterior pituitary are large and exhibit a wide-mesh Golgi. In the migrant males on the same date, the cells are smaller, most of them show a smaller meshed Golgi, and many cells are still in the "inactive" state.

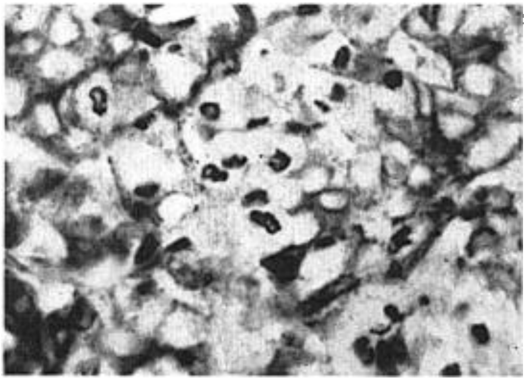

Fig. 16. Selected field under high power from sample 307 to illustrate further the enlarged type of Golgi apparatus and its variable shape. Photograph taken with 1.4 oil immersion objective, magnification 1850 (reduced ½); Nassonov-Kolatschev preparation.

This marked difference in the cellular structure of the pituitary corresponding with differences in testicular development was also demonstrated in the experiments with increased lighting. In experiment 3 (Wolfson, 1942) the increases in day length were begun on December 10. On January 18, 4 resident males were autopsied. They showed no deposition of fat, and their testes had developed to a combined volume of about 26.0 mm.^{3} Spermatids had already appeared in the tubules, and a few were already metamorphosing, but there were no mature spermatozoa. The Golgi apparatus in the pituitaries of these birds (numbers 307, 308, 309, 310) is illustrated in figures 13, 15, and 16, and they demonstrate clearly the hypertrophied state. Migrant individuals in the same experiment were autopsied on January 11 and January 21. Their testes had attained a volume of about 4.5 mm.^{3} The characteristic cell within the tubule was the primary spermatocyte and the interstitial cells were present in their maximum development between the tubules. Both males which were autopsied had a heavy deposition of fat and averaged 20.0 grams in body weight. The pituitary in these birds did not approach the high degree of secretory activity exhibited by the pituitary of the residents. Most of the cells were smaller, some showing characteristically the "intermediate type" of Golgi, and others the solid, compact type. Occasionally a few cells did show an hypertrophied Golgi.

One control migrant was sampled on January 14. Its testes were at winter minimum, and the cells of the pituitary resembled those of the wild birds which were in the "inactive" state.

Discussion and conclusions.—The structural differences in the cells of the pituitary under natural and experimental conditions clearly demonstrate that in juncos (1) there is an increase in the activity of the pituitary when the birds are subjected to increases in day length, and that (2) the pituitaries of the residents and migrants respond differently to the same lighting schedule. This difference in the cycle of the pituitaries in residents and migrants could be interpreted as a difference in the spontaneous rhythm of the pituitary, or it could be interpreted as an inherent difference in the response of the gland to external conditions in the environment. On the basis of the data obtained in the experiments, I conclude that the cycle of the pituitary is not spontaneous. Rather, the pituitary responds to changing external conditions, in this case the factor of day length. If it were true that the cycle was spontaneous and inherent, it should not have been possible to produce such a marked alteration in the rate of the gonadial or pituitary cycle by means of artificial increases in day length.

In this cytological study of the pituitary, our purpose has not been to determine the function of the Golgi apparatus or its role in the secretory cycle, but merely to determine whether structural changes within the cells of the pituitary could be correlated with the development of the gonads. However, the data which we have obtained are in agreement with our modern knowledge of the function, structure, and cyclical changes of the Golgi apparatus as presented by Hirsch (1939), Bourne (*loc. cit.*), and Kirkman and Severinghaus (*loc. cit.*).

According to current interpretation the condition of the Golgi which we described for birds with minimum testes indicates that the cell is not actively secreting. The solid, compact state would be equivalent to the pre-substance of Hirsch. These pre-substances according to Hirsch's theory build the network, and the product of the cell is formed in the internum. This network phase, with an osmiophobic internum and an osmiophilic externum, indicates a more active cell which is probably secreting, or at least forming the secretory product. This phase was seen in the juncos whose testes were in or approaching breeding condition. It is generally agreed that Golgi systems perform work in hypertrophy and the fluid, osmiophobic central portion enlarges as the product is formed.

The increase in the activity of the pituitary of juncos involves most of the cells in the gland and not one type or group of cells. The basophils are generally regarded as the source of the gonadoptropic hormone and judging from the growth of the testes one would expect them to show a state of high secretory activity. Concomitant with the recrudescence of the testes, large deposits of fat occur in the migrants, and this change in metabolism is no doubt related to a change in the functioning of the thyroid gland. In addition, other endocrine glands are probably involved. Hence, one expects that the increase in the secretory activity of the pituitary would involve most of the cells and not merely one cell type.

One further matter is worthy of mention. In rats, Severinghaus (1933) discovered that there was a difference in the Golgi apparatus in the chromophobe and chromophil cell types (acidophils and basophils). In the acidophil the typical Golgi is a basket-like network closely applied to one side of the nucleus like a cap, whereas in the basophil it is a spherical network in the cytoplasm and separated from the nucleus. In the junco both of these types have been observed, but it cannot be stated at present whether each type is restricted to a particular chromophil because we had no success in counterstaining for the differentiation of acidophils and basophils. All standard methods were used, and whereas sections of rat pituitary could be counterstained, those of the junco could not. Some modification in technique is probably necessary. Schooley and Riddle (1938), working with pigeons, and Payne (1942) working with fowls report that the chromophils cannot be distinguished by means of the Golgi apparatus.

BODY WEIGHT IN RELATION TO MIGRATION

The most extensive contributions to the study of bird weights are those of Baldwin and Kendeigh (1938) and Nice (1937, 1938). Both of these studies are highly organized to segregate the important facts, yet neither author gives a determinate account of the relation of body weight to migration. Remarks and data pertaining to migration are included for the most part in the sections on seasonal fluctuations in weight. The data are offered, therefore, from the point of view of monthly variation primarily and not migration. The purpose of the following account is to show explicitly the relation of body weight to migration and to demonstrate specifically that there exists in juncos and other passerines a significant correlation between an increase in body weight to a maximum and the beginning of the spring migration.

Designation of fat classes.—The large increase in body weight prior to migration would appear to be due to the deposition of fat, subcutaneously and intraperitoneally. Classes were defined to indicate the different amounts and distribution of the fat. These classes are, in increasing order, none, little, medium and heavy. In the "none" class the furculum and pterylae are practically devoid of fat subcutaneously. In the "little" class small amounts of fat are present in these places. In the medium class larger amounts of fat appear in the furculum and along the pterylae, and fat appears now in the axilla, on the shoulder, on the sides of the neck, on the lower back, and on the abdominal muscles. In a bird in the heavy class the amount of fat is increased in all of the aforementioned places, sometimes to such an extent that the even and uniform contour of the skin is altered by the protrusion of the fat masses. The fat becomes particularly conspicuous in this class on the lower back and in the abdominal region, where the addition of intraperitoneal deposition to that already present subcutaneously causes the abdominal region to bulge. To indicate extremes, plus and minus have been used occasionally for some of the classes.

The determination of the fat class is made when the bird is skinned, or in the living bird by blowing the feathers apart and examining the designated areas of the body.

Mean body weight of each fat class.—The mean weights of each fat class given in table 3 demonstrate that the deposition of fat is accompanied precisely by increases in body weight and that the differences among the classes are significant and can be recognized. If this were not true, the weight data, which were obtained independently of the fat data, would not show a similar increasing order with an almost constant increment.

Frequency of each fat class during winter months.—The data are presented in figure 17. They show clearly that there is a definite change in the frequency of occurrence of each of the fat classes in the population as the time for migration approaches. The heavy class occurs only in March, the month of departure for migrant juncos which have wintered in Berkeley. In November and December the "none" class predominates in the population, but by January the "little" class has become equivalent to it. The medium class is sparsely represented in these same months. In February and March the "none" and "little" classes are smaller than before and the medium class has increased.

Table 3

Mean weights of the fat classes*

Fat class			Subspecies *thurberi*	 *shufeldti*	 *oreganus*	Mean of all migrants
None	♂	Mean	16.54 (7)	16.55 (6)	17.15 (2)	16.62 (15)
		Extremes	15.5-17.6	15.2-18.5	16.5-17.8	
	♀	Mean	16.12 (5)	16.45 (4)	15.50 (2)	16.12 (11)
		Extremes	15.0-17.0	15.2-17.4	15.5-15.5	
Little	♂	Mean	17.44 (5)	17.16 (3)	17.90 (3)	17.50 (11)
		Extremes	17.0-18.0	16.0-17.9	17.3-18.9	**+5.29** per cent**
	♀	Mean	17.25 (8)	....	18.57 (4)	17.69 (12)
		Extremes	15.9-18.2	....	18.2-19.0	**+9.7** per cent
Medium	♂	Mean	18.28 (5)	18.20 (3)	19.70 (1)	18.41 (9)
		Extremes	17.2-19.0	17.6-18.8	....	**+10.7** per cent
	♀	Mean	17.60 (1)	17.20 (1)	19.7 (1)	18.16 (3)
		Extremes	....	....	....	**+12.6** per cent
Heavy	♂	Mean	19.13 (3)	20.30 (2)	20.05 (2)	19.72 (7)
		Extremes	19.0-19.3	19.6-21.0	19.1-21.0	**+18.7** per cent
	♀	Mean	18.65 (2)	19.50 (2)	19.10 (1)	19.08 (5)
		Extremes	18.5-18.8	19.2-19.8	....	**+18.4** per cent

* Only wild individuals are included. Numbers in parentheses represent the number of individuals. All weights are in grams.

** Per cent increase from "none" class.

One additional observation brought out by the data is that the females lag behind the males in arriving at the heavy class. This is in agreement with the experimental data which showed that the males reached the heavy class first. This lagging behind in the females in the preparation for migration would also explain why in many species the females migrate later and arrive on the breeding grounds after the males. Under experimental conditions there is no doubt that the females react differently to the same day-length schedule and there is no reason to believe that under natural conditions this difference in response of males and females to the same environmental conditions would not be exhibited.

Mean monthly weights.—Having demonstrated the monthly variations in the size of each of the fat classes and the mean weights of these classes, there remains the task of computing the mean monthly weights so that our data can be compared with those of Baldwin and Kendeigh, Nice, and other authors. The mean monthly weights for the migratory races of the Oregon junco, as well as other species, are given in table 4. From the lowest mean weight of 16.20 gm. in December there is an increase of 13.4 per cent to a mean weight of 18.37 gm. in March. This compares favorably with the 18.6 per cent difference in weights between the male migrants in the "none" class and those in the heavy class. A lower percentage of increase in the monthly mean weights is to be expected because of the variable composition of the population as a whole with regard to fat classes.

Fat deposition and body weight in the resident race, J. o. pinosus.—Further evidence which reinforces the conclusion that a large deposition of fat is closely correlated with migratory behavior is gained from a study of the resident population. In six years of study, not one resident has shown a heavy deposition of fat. Most of those collected during the winter show little or no fat; only a few have ever reached the medium class. In table 5 the mean monthly weights for *pinosus* are given. No regular increase in weight is shown, although there is a difference of 5.7 per cent between December and March. Weight data which are available in the literature for other resident populations confirm these observations and are discussed later.

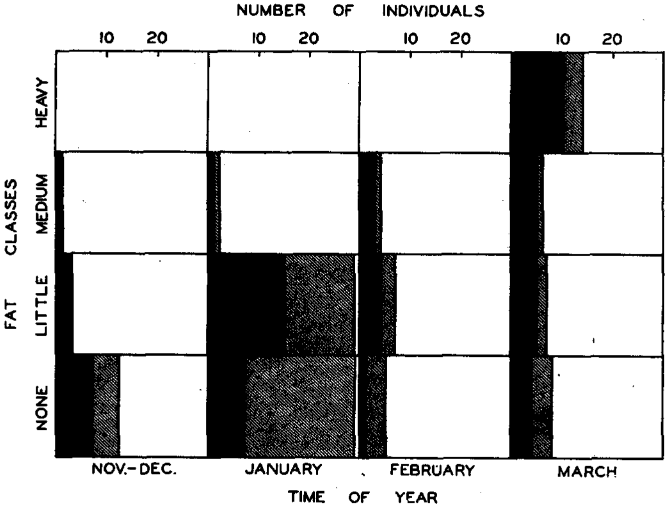

Fig. 17. Occurrence of fat classes from November through March. Solid black rectangles indicate males; rectangles with diagonal lines, females.

Fat deposition and body weight in experimental juncos.—One further line of evidence, the data from the experiments in migration, supports the aforementioned observations which were made on wild birds. The data have already been published (Wolfson, 1942) and may be summarized here. In the induced migration experiments the residents showed practically no fat deposition and no increase in weight. In marked contrast, the migrants showed an increase in weight equivalent to that which occurs under natural conditions and even exceeding it in some instances. Concomitant with this increase in weight was the deposition of fat, with the result that individuals in the heavy fat class were prevalent at the end of the experiment. These changes occurred within 50 days whereas under normal conditions they require approximately 100 days. In the delayed migration experiments the residents showed little or no deposition of fat, whereas the migrants retained, until their release in June, their heavy deposition of fat and higher body weight which was acquired usually by the first week in April. It should be emphasized that, from the time that the heavy fat deposition was acquired until early June when the birds were released, the testes had developed to breeding condition and contained mature spermatozoa. In the prevention of migration experiment the heavy deposition of fat was lost in July and there was then a decrease in weight. With the approach of the normal time for the fall migration in September and October the experimental birds, which were already on their wintering grounds, again showed a heavy deposition of fat and increase in weight. The data have been presented in table 1.

Conclusions.—On the strength of the evidence which has been presented, obtained both under natural and experimental conditions, it is concluded that an increase in body weight due to the deposition of fat precedes migration and that without this "preparation" migration is usually not undertaken. The bird of course does not prepare for migration in the sense that it foresees the energy requirements of the journey, but "it is prepared" at the proper time by the response of its endocrine glands to external factors in the environment. The most important of these is the continuous daily change in the proportions of the daylight (day length) and darkness (night length). The response of the endocrine system results in the change in the metabolism which in turn leads to a heavy deposition of fat. Furthermore, it seems that the air temperature is not a controlling factor in the deposition of fat. Experimental birds have shown a heavy deposition of fat in January, June, September and October. The mean temperatures of these months for Berkeley are, respectively, 48.0° F., 60.8°, 62.0°, and 59.9°.

Findings of other authors. Migratory species.—Our conclusions are at variance with those of Baldwin and Kendeigh, and Nice. It becomes necessary, therefore, to examine their data in order to determine whether the migratory species which we studied are unique, or whether their conclusions are unwarranted, possibly because of faulty interpretation of data and errors of omission. The House Wren and Song Sparrow upon which they worked have been investigated more thoroughly than any other species in this country and yet the recorded data which are relevant to the present problem are not consonant with data obtained in the present investigation. In addition the other pertinent literature must be considered.

Golden-crowned Sparrow. The most extensive weight data in the literature for a migratory species are those of Linsdale and Sumner (1934*a*, 1934*b*) on the Golden-crowned Sparrow (*Zonotrichia coronata*). A large number of individuals of this species winter at Berkeley and are easily trapped. They leave there usually at the end of April and early May for their breeding grounds in Canada and Alaska. A total of 1422 records for 286 individuals were recorded in one study of birds in the wild (1934*b*). In the other study (1934*a*) records were obtained from 53 birds which were kept in captivity.

The authors found that in birds in the wild there was a peak in weight in January and another considerably higher one preceding migration in May. The mean monthly weights are given in table 4. They show that the January weight is 6.3 per cent higher than the December weight, whereas the May weight is 20.8 per cent higher. This exceeds the 13.4 per cent increase in weight prior to migration which was found in the Oregon Junco. However, the changes in body weight in the two species during the winter is different. In figure 12 the winter weight curves are plotted on the basis of per cent change from December body weight. The sharp, sudden increase in weight in the Golden-crowned Sparrow exceeds greatly the rate of increase in the Oregon Junco and all of the other species as well. No birds were autopsied in this study by Linsdale and Sumner and they offered no explanation as to the cause of this seasonal increase in weight.

The study of the birds that were kept in captivity confirmed the observation that throughout the spring there was a progressive increase in weight up to the time of migration. In addition, it was shown that the birds maintained their May peak in weight until July 22, when the last group of birds was released. A similar observation was made in our study of the Oregon Juncos in the delayed migration experiment, where the high weight was maintained until 60 days after the usual time of departure.

In this study of captive Golden-crowned Sparrows, four, whose weights were recorded daily from April 16, were autopsied on June 18. The healthiest and most normal bird of the four was a male which had exceeded the others in body weight for the duration of the experiment. It was in good plumage, its testes were 8 mm. in length (approximate breeding condition), it weighed about 38 grams, and it was exceptionally fat. The significance of this fat is not discussed by the authors.

Fox Sparrow. Another migratory species for which reliable weight data for each month are available in the literature is the Fox Sparrow (*Passerella iliaca*). These data were obtained by Linsdale and Sumner (1934*b*) along with the data on the Golden-crowned Sparrow. The birds were not identified as to sex or subspecies. The mean monthly weights are recorded in table 4. They demonstrate that a peak in weight is reached in December and that an increase in weight occurs in April and May preceding migration. The magnitude of this increase (March to May) is 12 per cent which is comparable to the increase in the other species. Calculating from the December weight, however, the percentage of increase is only 4.9 per cent. I think that the marked differences in the curve for December, January, and February, when compared with the other species, may be due in large part to the fact that the weight data include at least three subspecies of Fox Sparrows which are known to winter at Berkeley. However, the weight records of one individual which are available agree generally with the curve in figure 12 which is based on 711 records for 91 birds. This would suggest that the Fox Sparrow does differ from the other species in having a higher weight in December than during the other winter months. More data should be available, and preferably for one subspecies, before any conclusions can be drawn. In spite of these differences in the early winter months, there can be no question that the salient observation—the increase in weight preceding migration—is in complete agreement with the data for the other species.

Tree Sparrow. In her study of the Tree Sparrow (*Spizella arborea arborea*), Baumgartner (1938) recorded and studied seasonal variations; those in body weight and fat are pertinent to the present problem. With regard to weight she concluded that "a more or less uniform weight is maintained throughout the winter months, culminating in a sudden increase at about the end of February, after which there is a gradual decrease during the spring migration." In an earlier report (Heydweiller, 1935), she had written: "the maximum figures [body weight] are not attained again until just preceding the spring departure during the first two weeks in March. At this time the males average 21.3 grams, the females 20.2 grams. Both males and females in late March and throughout April are some ten per cent lighter. Again the question arises whether this phenomenon is due to an influx of younger birds or to the hardships of migration." The average weights just quoted are higher than the mean monthly weights which I calculated for table 4 and probably represent a more accurate statement of the average weight reached before migration ensues. Using her average weight for males, the increase in weight from December would be 15.3 per cent instead of the 10.9 per cent listed in the table. This increase in weight is comparable with that demonstrated in the other species.

The loss of weight in April is not in agreement with the data from the other migratory species. Data from Hicks in Ohio (given by Baumgartner) indicates increasing weights up to April 2, the last date of collecting. I think that the lower weight in the April birds of Baumgartner can be explained by the fact that these birds were transients and, therefore, are not comparable to the winter residents of Ithaca which leave during the first two weeks in March. That these birds are transients is deduced from Baumgartner's comments and especially from the fact that in February and March the sex ratio of birds collected is two males to one female, whereas by the first week in April there are three females to every male. Since the females leave their wintering grounds after the males the only conclusion which can be drawn is that migration is underway and that the Tree Sparrow population at Ithaca begins to change in composition by March 15. The lower weight during migration indicates that the transients do not maintain their high pre-migratory weight.

Table 4

Mean monthly weights of migratory species from December to May, listed in order of abundance of data

Species and Authority	Dec.	Jan.	Feb.	Mar.	Apr.	May
Zonotrichia coronata (Linsdale and Sumner, 1934*b*)	29.36 (50)[2]	31.22 + 6.3[1] (55)	29.53 + 0.5 (310)	29.52 + 0.5 (542)	30.94 + 5.4 (228)	35.47 + 20.8 (15)
Passerella iliaca (Linsdale and Sumner, 1934*b*)	33.95 (26)	33.05 — 2.7 (46)	32.03 — 5.7 (270)	31.82 — 6.3 (163)	33.42 — 1.6 (48)	35.64 + 4.9 (10)
Spizella arborea arborea (Baumgartner, 1938)	18.47 (9 ♂♂ ad.)	19.13 + 3.6 (12 ♂♂ ad.)	20.29[3] + 9.9 (26 ♂♂ ad.)	20.50 + 10.9 (15 ♂♂)	19.54 + 5.8 (27 ♂♂)	....
Junco oreganus subsp. (Wolfson)	16.20[4] (5 ♂♂)	17.27 + 6.6 (21 ♂♂)	17.50 + 8.1 (8 ♂♂)	18.37 + 13.4 (21 ♂♂)	....	....
Zonotrichia leucophrys pugetensis (Wolfson)	27.00[5] (........)	27.87 + 3.2 (6 ♂♂)	27.82 + 3.0 (6 ♂♂)	28.83 + 6.8 (28 ♂♂)	31.23 + 15.7 (7 ♂♂)	....

[1] Change from December weight expressed in per cent.
[2] Number and source of weight records. No segregation as to sex or age unless stated.
[3] High weight due to 12 birds averaging 21.2 caught on Feb. 26; without these weight would be 19.5.
[4] November records included due to small numbers.
[5] Interpolated from Blanchard's data (1941).

With regard to fat deposition, Baumgartner writes: "Correlated with weight is the amount of fat encircling the body. While no pronounced change could be traced through the winter months due to the range of individual variation [no fat classes were used] there was a marked difference between winter and summer birds." No fat birds were collected during the nesting period, and "fat was not observed again until August 8, when family cares were practically over. In juvenal birds it was first observed on August 1 in a fully fledged young. On a well padded specimen of March 20, 1935, the fat was scraped off as clean as possible and found to weight approximately 1.5 grams or 7.73 per cent of the total weight (19.4 g.). The fat is found in well defined paths corresponding to the feather tracts, encircling the neck and upper breast, and especially on the lower belly and anal region."

Again, the increase in weight and the correlation with fat deposition is in close agreement with the data for the Oregon Junco. Because of the earlier initiation of migration in the Tree Sparrow at Ithaca, New York, one expects an earlier increase in weight than in the Oregon Junco, and this is indicated by the data in figure 18.

White-crowned Sparrow. In a recent study of two races of the White-crowned Sparrow, *Zonotrichia leucophrys pugetensis* which is a winter resident in Berkeley, and *Zonotrichia leucophrys nuttalli* which is a permanent resident, Blanchard (1941) contributes data which are in accord with those for the Oregon Junco. She writes (page 88): "In *pugetensis* the prenuptial molt and the recrudescence of the gonads are accompanied by the assumption of large amounts of fat. This increase is so great that the body weight of adults increases from an average of 26.8 gm. for adult males with no fat to an average of 32.6 gm. for those with the maximum amount, a 21.6 per cent increase." She did not present the mean monthly weights. However, because of the large number of White-crowned Sparrows in the collections of the Museum of Vertebrate Zoology, I was able to calculate these weights and they are recorded in table 4. They confirm the increase in weight preceding migration and its coincidence with the increase in the amount of fat deposition.

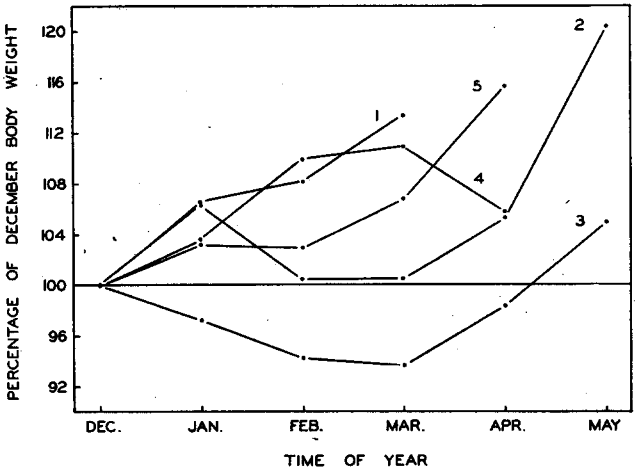

Fig. 18. Changes in body weight from December through May for five migratory species, expressed in terms of percentage of December body weight. 1, Oregon Junco; 2, Golden-crowned Sparrow; 3, Fox Sparrow; 4, Tree Sparrow; 5, Puget Sound White-crowned Sparrow.

Blanchard also segregated her birds into fat classes. These classes and the average weight for adult males in each class are as follows: no fat, 26.8; little fat, 28.0; moderate fat, 29.1; fat, 29.3; very fat, 32.6. Judging from the average weights and her descriptions of the classes it seems to me that her "fat" class is not significant and probably should be combined with her "very fat" class. If this is done her classes are in agreement with those designated for juncos, and more significantly, the magnitude of the weight changes between the classes is similar to that in juncos. In table 5 is recorded the average weight in grams for each fat class and the difference in weight between the "none" class and each of the other classes, expressed in terms of per cent.

The close agreement of these data seems to establish the validity of these classes beyond any reasonable doubt, and by applying them to other passerine migrants their occurrence as a general phenomenon preceding migration can be determined.

Table 5

Average weight for each fat class and increases expressed in per cent for the Oregon Junco and the White-crowned Sparrow

	None	Little		Medium		Heavy	
J. oreganus	16.6	17.5	+5.3	18.4	+10.7	19.7	+18.7
Z. l. pugetensis	26.8	28.0	+4.5	29.1	+ 8.6	30.9	+15.3

In this connection, studies of wild Golden-crowned Sparrows, which were trapped along with the juncos, showed that the increase in weight preceding migration, which was so soundly demonstrated by Linsdale and Sumner, is due to fat deposition. In addition, under experimental lighting conditions, such as those to which the juncos were subjected, the Golden-crowned Sparrows showed the spring pre-migratory changes such as fat deposition, prenuptial molt, and recrudescence of the gonads in October and November. Also, Golden-crowned Sparrows which were prevented from undertaking a spring migration in 1944 still showed a heavy deposition of fat as late as July 15.

With regard to the resident race, *Z. l. nuttalli,* Blanchard states that they may "lay on a little fat, but no such phenomenon as that described for *pugetensis* accompanies the recrudescence of the gonads. Of 60 males with testis volumes comparable to the Berkeley *pugetensis* collected from January to March in all years, 44 had no fat, 13 had little fat, and only 3 had moderate fat."

Additional species. The presentation of the data from the literature up to this point has included only those migratory species for which adequate monthly weight records were available. There are also in the literature weight data which are not as extensive and hence not as cogent as those already presented, but which merit consideration nevertheless because of relevancy. Groebbels (1932) presents monthly weight data for three captive male Chaffinches (*Fringilla coelebs*), one of which lived for three years. Niethammer (1937) states that the Chaffinches which occur in Germany leave in September and October and return in March and April. Groebbels' data show that preceding the normal time of spring migration the birds showed consistently increasing weights to a maximum in March or April, and this was shown three times by one individual which lived for three years. The maximum increase in "pre-migration" weight over the minimum winter weight in this individual averaged 33 per cent for the three years. A study of the species as a whole would probably show a much lower average increase. The other individuals showed increases of equal magnitude, and in one case an increase of 45 per cent was recorded from January to the end of April. Preceding the normal time for fall migration the weights again increased after having dropped to lower levels during the summer months. The amount of increase, however, is less than half of that which occurred prior to the spring migration.

For one Whitethroat (*Sylvia communis*), Groebbels gives the following records: March 14, 21 grams; April 1, 18 grams; May 7, 14.5 grams; it maintained this low May weight until autumn, when it weighed 22 grams. *Sylvia communis* is a migrant in Germany.

Zedlitz (1926) made a study of monthly variations in the weight of several European species. Although it is generally true as Baldwin and Kendeigh (1938:431) write that "with *few exceptions* [italics mine] all species weighed most in winter and early spring, decreased during the breeding season, and then increased during the following autumn," the exceptions nevertheless are very significant since it happens that they represent non-migratory species. The winter residents which Zedlitz studied were the Brambling (*Fringilla montifringilla*) and the Fieldfare (*Turdus pilaris*). Both of these showed large variations in weight and fat deposition during the winter. The data are not complete enough, however, to warrant a comparison of monthly weights.

The permanent residents for which comparable data are given are the Magpie (*Pica p. pica*), the Yellow-hammer (*Emberiza c. citrinella*), the Willow Tit (*Parus atricapillus borealis*) and the Marsh Tit (*Parus p. palustris*). The data for these four species, although incomplete, do not indicate any great variation in weight in the winter and early spring months such as is indicated by the data for the winter residents. Data are also given for transients, and although they are far from being complete, they indicate increases in weight suggestive of those shown by the winter residents, yet totally unlike data for the permanent residents.

Merkel (1938) in his studies in the physiology of bird migration demonstrated that there is a close correlation between a high body weight and the "migratory period" of captive birds. The "migratory period" is determined by the amount of movement (restlessness) exhibited by the bird and is recorded automatically. There is no close agreement between the duration of the recorded "migratory period" and the duration of the normal period of migration, but this is to be expected in captive birds. Merkel also demonstrated that after the breeding season weight increases until a peak is reached at the beginning of the fall migration. This is in agreement with our comparable data. Nice, however, in reviewing Merkel's paper comments on this conclusion as follows (1939:45): "This, however, was not true of the Song Sparrows I studied, nor does Kendeigh's work corroborate it. It is difficult to get any consistent picture from the author's results between weight of the bird, amount of food taken, and migratory state." An analysis of the seemingly contradictory data of Kendeigh and Nice will be presented later.

Resident species.—It was demonstrated that the resident populations of the Oregon Junco (*J. o. pinosus*) and the White-crowned Sparrow (*Z. l. nuttalli*) do not show any fat cycle and consequently no marked seasonal variation in weight. Weight data for other resident passerine species are available in the literature and these have been summarized in table 6. A study of the table reveals the following: (1) Not one species shows an increase in weight during the winter or spring which is equivalent to that in migrants; (2) as the breeding cycle proceeds there is a loss in weight; (3) the monthly variations in weight are small and in some cases not significant.

Data and conclusions of Nice.—Inasmuch as most ornithologists would agree that more data have been recorded for the Song Sparrow than for any other American species, with the possible exception of the House Wren, it is puzzling in view of our observations that the weight data presented by Nice (1937) indicate that "almost no difference was found in the weights of residents, summer residents, transients and winter residents *taken at the same time of the year* [italics mine]. The noon weights of 126 males in March and April gave the following averages: 52 residents 22.8 g., 52 summer residents 22.6 g., and 22 transients 22.4 g." (1937:20). After examining the data it is my contention that her conclusion is unwarranted, that the mean monthly weights presented by her (1937, table II, p. 21) are not representative for *each* of the populations of different status and that her data cannot be accepted as valid when compared with other species wherein data for resident and migratory populations are segregated. The following reasons are offered in support of this contention. (1) The mean monthly weights as recorded by Nice include four different and variable populations—permanent residents, summer residents, winter residents and transients. (2) She included individuals of all four populations in calculating the mean monthly weight for each sex in the species because of the similarity in the average weight of the males *of three* of these populations *for only the combined months of March and April.* (3) The average weight of the winter residents apparently was not calculated separately at any time, and *a priori* was assumed to be similar to that of the others.

Nice concluded from her weight data of summer and fall individuals that weight reaches a "minimum in late summer and fall starting to increase in December." It follows, therefore, that there was no increase in weight in the summer residents before their departure in late September and October. The objections which were raised above are applicable as well to this conclusion.

On these grounds, the weight data as presented by Nice for the Song Sparrow, a partly migratory species, cannot be considered as contradictory to the data which have been presented for other migratory species, particularly with respect to their status as winter residents.

Nice (1937:23) comments that the yearly weight curve for Partin's House Finches (see table 6) "is fairly similar to that of my Song Sparrows, especially the marked increase from December to February." This similarity with a resident species with a "marked" increase of 3.2 per cent leads one to the conclusion that most of Nice's weight data were obtained from permanently resident individuals. An analysis of her data supports this conclusion. A total of 746 weight records was obtained from 455 banded Song Sparrows. Of the individuals which she banded, 57 per cent were residents and summer residents, 15 per cent were winter residents, and 28 per cent were transients. Further, it seems that summer residents and residents are present in about equal numbers (average for 6 years). From the foregoing data it is evident that during the winter months, December through February, the ratio of permanent residents to winter residents is about 2 to 1. In all probability it may be even higher, because the determination of winter resident individuals is extremely questionable. Of 70 banded "winter residents" only two returned to Interpont. This ratio of two permanent resident individuals to each winter resident individual and the assumption that multiple weight records per bird were taken from more permanent resident individuals than from winter resident individuals, would account in part at least for the similarity between the weight curves of the House Finch, a permanent resident, and the Song Sparrow.

In her later paper (1938) on the biological significance of bird weights, Nice asserts that the weight curve of the Song Sparrow is different from that of the Tree Sparrow, Golden-crowned Sparrow and Fox Sparrow. She does not consider that the lack of agreement among the data may be due to the fact that the weight data for these species were obtained almost exclusively from winter residents, whereas her data were not.

In discussing winter weight Nice writes as follows (pp. 3 and 4): "That many species respond to cold of winter by putting on a coat of fat is shown by the preponderence of cases in which weight increases at this season. The Song Sparrows on Interpont gained weight in December, reaching their peak in January. Individual males sometimes gained as much as 25 to 44 per cent of their April weights" (since present during month of April are we to assume that these are residents?). Is it possible to correlate the increase in weight with fat deposition when Nice presents no data on the fat condition of the birds which she studied? It is known that birds were not collected for autopsy in her studies, and she does not describe any other method for determining the fat condition.

In summarizing the weight data in the literature for the winter months, Nice classifies one group of birds as showing little change in weight in the winter. Among these is the Chinese Tree Sparrow (*Passer saturatus*). Ernst Mayr, as stated by Nice, suggested that "the lack of gain may be correlated with the habit of sleeping in holes." Other species listed in this group, which according to Nice sleep in cavities, are the Carolina Chickadee (*Parus c. carolinensis*), the Tufted Titmouse (*Parus bicolor*), the Black-capped Chickadee (*Parus a. atricapillus*), and the Marsh Tit (*Parus p. palustris*). It is my contention that the lack of gain in weight in winter (and any other seasonal variations in weight) in these species is not correlated with their roosting habits, but rather with their status as residents. This contention, however, must not be construed as claiming that the roosting habits of an individual cannot influence its weight. Any correlation between roosting habits and changes in body weight which might be demonstrated would probably be manifest in the variations in the daily weight cycle and not in the variations in the annual weight curve.

Table 6

Mean monthly weights of resident species from December to May, listed in order of abundance of data

Species and Authority	Dec.	Jan.	Feb.	Mar.	Apr.	May
Carpodacus mexicanus frontalis (Partin, 1933)	21.5 (37♂♂)	21.6 + 0.5[1] (59♂♂)	22.2 + 3.2 (80♂♂)	20.9 — 2.8 (85♂♂)	20.9 — 2.8 (17♂♂)	20.8 — 3.3 (57♂♂)
Pipilo maculatus falcifer (Linsdale and Sumner, 1937)	39.51 (5♂♂)	39.06 — 1.1 (18♂♂)	39.03 — 1.2 (44♂♂)	38.19 — 3.3 (24♂♂)	38.07 — 3.6 (9♂♂)	40.28 + 1.2 (3♂♂)
Passer domesticus (Kendeigh, 1938)	28.4 (7♂♂)	29.9 + 5.3 (34♂♂)	28.6 + 0.7 (19♂♂)	29.7 + 4.6 (6♂♂)	26.5 — 6.7 (1♂)	27.2[2] — 4.2 (5♂♂)
Passer montanus saturatus (Shaw, 1935)	20.5 (16♂♂)	20.1 — 2.0 (12♂♂)	21.8 + 6.3 (4♂♂)	21.5 + 4.9 (8♂♂)	20.1 — 2.0 (8♂♂)	21.6 + 5.4 (5♂♂)
Zonotrichia leucophrys nuttalli (Wolfson)	30.60 (8♂♂)	30.19 — 1.3 (21♂♂)	28.65 — 6.4 (12♂♂)	28.03 — 8.4 (7♂♂)	....	....
Dryobates pubescens (Kendeigh, 1938)	....	27.9 (3♂♂)	26.9 — 3.6 (3♂♂)	27.4 — 1.8 (5♂♂)	28.2 + 1.1 (6♂♂)	28.3 + 1.4 (19♂♂)
Junco oreganus pinosus (Wolfson)	15.80[3] (8♂♂)	16.76 + 6.0 (6♂♂)	15.06 — 4.7 (3♂♂)	16.70 + 5.7 (2♂♂)	....	....

[1] Change from December weight expressed in per cent.
[2] June records included.
[3] November records included due to small numbers.

To summarize our evaluation of Nice's work, it may be stated (1) that her weight data on the Song Sparrow enabled her to calculate a "standard" (annual) weight for this species, (2) that her data on seasonal variations in weight cannot be considered contradictory when compared with that of other species where the weights of migrant and resident individuals are tabulated separately, and (3) that in considering the biological significance of birds' weights she failed to recognize the importance of the seasonal status of an individual as a factor in influencing its weight.

Data and conclusions of Baldwin and Kendeigh.—Like Nice, Baldwin and Kendeigh (1938) included the important studies in their review of the relevant literature, but did not consider carefully the migratory status of a species as an important factor in monthly variations in body weight. This is most apparent from their view of the work of Linsdale and Sumner, but it is also substantiated by their discussion of other data in the literature. They state (p. 432): "Linsdale and Sumner (1934*b*) found in a large number of weighings of the Golden-crowned Sparrow and the Fox Sparrow an increase in weight from October until a peak was reached in mid-winter (about January) and that another even higher peak was reached in May just before the spring migration. . . . In a later study of Spotted Towhees, Linsdale and Sumner (1937) found somewhat similar monthly variations in weight on the basis of more fragmentary data, although they state the male towhees did not show a *peak in weight just before migration in the spring* [italics mine] as did the other two species with which they worked." Apparently, Baldwin and Kendeigh consider the Spotted Towhee a migrant, and since the spring weights of these three migrants do not agree in demonstrating a peak in weight prior to the spring migration, they do not indicate that such increase is a fundamental variation in weight. However, they overlooked the salient fact that the Spotted Towhee is not migratory, but is a permanent resident in Berkeley. Linsdale and Sumner recognized that their data for the Spotted Towhee were not as complete as those for the other species, but they considered "them worthy of summarizing because this species is permanently resident, while the other two are migratory. . . ." Moreover, I cannot agree with the statement of Baldwin and Kendeigh that the variations in the Spotted Towhee were "somewhat similar" to those in the migrant species. An examination of table 4 and table 6, where the monthly weights from December through May are recorded for the three species in question, reveals the differences in the amount and trend of these monthly variations.

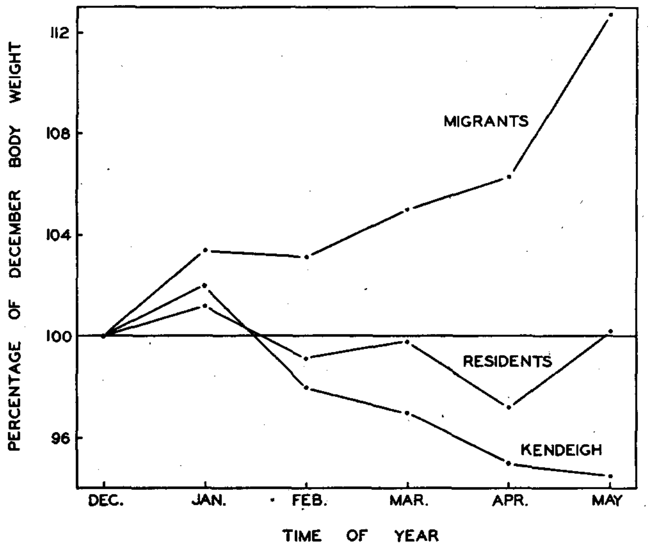

Fig. 19. Comparison of changes in body weight of residents and migrants from December through May, and comparison of these with corresponding part of annual weight curve as computed by Baldwin and Kendeigh. Curves for residents and migrants computed from the data in tables 4 and 6.

From their original data which are summarized in table 5 (pp. 436-445), Baldwin and Kendeigh conclude (p. 435): "An average of all species clearly shows the minimum weight in July. In general, the weights increase month by month until mid-winter, then decrease again during the spring. . . ." A generalized curve based on monthly averages for all species is given wherein each month's weight is expressed in percentage of the average weight during the three principal breeding months of May, June and July. I have recorded in figure 19 that part of the curve which is most relevant to this study, the part from December through May. To make the curve comparable with our available data it is plotted on the basis of percentage of December body weight. The character of the curve, however, remains unaltered. Also plotted in the same manner in this figure are the averaged monthly changes in weight of all the migrants and residents listed in tables 4 and 6.

The marked differences in the curves of the residents and migrants demonstrates conclusively that the curve drawn by Baldwin and Kendeigh cannot be considered applicable to migratory species. Therefore, their data and conclusions cannot be considered contradictory to those which we have presented.

Moreover, in view of the great differences in the spring weight variations among residents and migrants and the fact that these authors have combined the weight data of residents and migrants, their curve does not represent an accurate weight curve for residents. However, the close similarity in the character of the resident curve and that of Baldwin and Kendeigh suggests that their data were not equally distributed among the species of different status, but were obtained predominantly from residents. An examination of their data reveals that this is true. An analysis of the 28 species which were used to calculate their curve is given in table 7; it indicates clearly the preponderance of permanent resident and summer resident species.

Table 7

Analysis of 28 species used by Baldwin and Kendeigh to calculate an annual weight curve of birds

Number of species of each status

Month	Permanent Resident	Summer resident	Winter resident	Transient
Dec.	2	....	1	....
Jan.	4	....	1	....
Feb.	4	....	2	....
Mar.	6	3	2	....
Apr.	6	8	2	2
May	6	10	....	2

Only those species are included for which more than four weight records were available.

When discussing the possible causes of monthly weight variations, Baldwin and Kendeigh state (p. 434) that "the suggestion that birds, by becoming fat at certain seasons, unconsciously foresee migration or breeding or wintering conditions of [*sic* =or?] any other energy requirement seems unjustified." Obviously, the bird does not foresee the requirements of migration, but our studies have shown the close correlation between a heavy deposition of fat and the initiation of migration and I cannot agree consequently with the implications of their conclusion. It follows also from our analysis of their data that the conclusion itself is unwarranted. No data were presented on the fat condition of the birds, and one could not expect to find a peak in the body weight of migrant individuals prior to the spring migration when the weight curve was calculated primarily from the weight data of permanent residents and summer residents!

CONCLUSIONS AND DISCUSSION

The annual stimulus for migration.—From the results of the experiments in migration and the related studies, it is apparent that the stimulus which each year induces juncos and other birds to leave their wintering grounds is not one which can be produced suddenly by momentary or transitory variations in their natural or experimental environment. Rather, the stimulus results from the physiological response (internal factor) of the bird to regular changes in day length (external factor) over a *long period* of time. Ultimately, the physiological response of the bird, as manifested by the growth of the testes, the increase in the secretory activity of the pituitary gland, the deposition of large amounts of subcutaneous and intraperitoneal fat, and the concomitant increase in the body weight, reaches a state that will enable the bird to meet the energy requirements of migration. Then the behavior patterns which initiate the migratory flight are released.

Since experimental birds which did not have a heavy deposition of fat failed to migrate, it is possible to conclude that the deposition of a definite amount of fat is the internal stimulus for migration. However, I think it is best to regard fat deposition as a primary part of a general, metabolic internal stimulus and as an excellent indicator of a readiness to migrate. With further study other manifestations of the altered physiological state which precedes migration can probably be found, and it is improbable that any one part of this physiological state will be the "sole stimulus" for migration. The parts of the internal stimulus which have been studied indicate that some one part, such as the pituitary, may be sufficiently dominant in the functioning of the organism to determine ultimately the total physiological state, and hence the type of behavior exhibited. Nevertheless, at the present time it seems best to regard the total physiological state with its various manifestations as the internal stimulus for the spring migration.

From these conclusions and other evidence which has been presented (Wolfson, 1942) it follows that the gonads or the reproductive system cannot be considered as the primary source of the annual stimulus, as held by Rowan and other authors. Further, there is no factual basis for the belief that migration is a "phase" of the reproductive cycle. Migration and breeding involve different patterns of behavior and are separate entities in avian life cycles. In the phylogeny of an originally resident species migration must have been imposed on an already existing breeding cycle and correlated with it through the action of the environment and natural selection.

Relation between external and internal factors.—In the migration experiments, increases in day length induced changes in the physiological state of the birds to the point where they undertook a northward migration two months earlier than usual. From these results, it is concluded that under natural as well as experimental conditions, external factors, in this case day length, can initiate and maintain progressive changes in the endocrine system and metabolism of migratory juncos. It follows, therefore, that these changes do not arise spontaneously or automatically, nor are they independent of the environment for their basic rhythm.

The cyclic nature of the secretory activity of the endocrine system can be regarded as an inherent rhythm since it is a result of the heritable properties of the glandular tissues. It must be emphasized, however, that an inherent rhythm does not necessarily arise spontaneously or automatically. This point can best be illustrated as follows: When resident and migrant individuals were subjected to the same experimental lighting conditions, the residents showed a must faster rate of development of the testes and no fat deposition; the migrants showed fat deposition and a much slower rate of gonadial growth. In each case the response was *inherent* and was limited and controlled by the genetic constitution of the individuals involved. In each case as well, however, the response was definitely produced by the manipulation of the external environment. Consequently, the inherent rhythm of the endocrine system is not regarded as being automatic or spontaneous, or as arising from causes which are independent of environmental stimulation. Certainly all birds will not be identical in this regard, but in juncos and related species there can be no doubt of the causal relationship between the external and internal factors which are involved in producing the annual stimulus for migration.

The external factor in the experiments which was responsible for the physiological changes was the progressive increases in day length. It is not known, however, how the increases in day length produce the physiological changes in the bird. That the nervous system is the mediator between the environment and organism seems certain; and it seems probable that the relative daily proportion of sleep and wakefulness may be a factor in stimulating and regulating the endocrine rhythm. A review of the problem has already been given (Wolfson, 1941).

Bearing of these conclusions on the problem of individual or partial migration.—In the past the status of a species has been recorded as migratory or non-migratory with little examination of the populations within the species and their particular status. It is becoming clear, however, that migration as a type of behavior is not always exhibited by all the individuals of a species, or even a population. Further, there are reports of individuals which change status from one year to the next, or as they age.

With regard to populations within a species, our own studies of the Oregon Junco and White-crowned Sparrow bear out the differences in behavior and the differences in physiological response to identical environmental conditions in migratory and resident populations. In these two instances the migrant and resident populations are accorded subspecific rank and can be separated morphologically with a good amount of success by comparing them with known series of skins. Recently, however, Bullough (1942) has shown that starlings in England can be separated into migrant and resident populations because of differences in their reproductive cycles, but he was unable to obtain sufficient morphological evidence to enable him to identify the two types. On the basis of physiological differences he recommended the designation of the two populations as subspecies. In effect, they are physiological races.

The significance of these races of different status within a species is that the status of many of our so called "permanently resident" species should be carefully examined for populations of migratory status. There is highly suggestive evidence derived from bird banding that some permanently resident species also "migrate." In addition to the evidence derived from banding, more conclusive evidence for true migration such as differences in the reproductive cycle and fat deposition can now be obtained. With this additional evidence perhaps these migrant populations could be accurately defined. Once discovered, a careful study of the population might also yield morphological differences. If morphological differences are found, the problem of defining subspecies should not be a difficult one. If they cannot be found, however, we are faced with the question of whether or not subspecific rank should be given to populations which differ sufficiently physiologically and psychologically so that they occupy different breeding areas.

In this connection, one item of extreme interest must be mentioned. Dr. Lawrence E. Hicks, who has studied intensively the movements of the starlings in this country, informed me that he has also made studies of the reproductive cycles of the various populations of starlings in Ohio. He has found differences comparable to those which we have found for resident and migrant juncos, and his data suggest as well a difference in fat deposition! (Bullough does not mention fat deposition in his studies of the starling, nor did he record their weight.) This must mean that the two "races" of starlings which Bullough describes are represented in this country, although at present they may not be discrete populations.

Heretofore, data obtained through banding birds were of necessity relied upon heavily for determining the status *of individuals*. From our studies, it is clear that fat deposition and any increase in body weight are diagnostic of migrants in several species. This information can now be used to determine more accurately the status of an individual. It was possible before to err completely in defining an individual as a winter resident or a migrant by relying on its presence or absence in a small restricted area. Now, by examining these individuals and recording their weight and fat deposition on the wintering grounds or breeding grounds it should be possible to determine their status more accurately. The employment of our findings as suggested is the only way in which their validity and general application as criteria for indicating a readiness to migrate can be determined. There is good reason to believe, judging from the California species which have been studied, that they will be valid and applicable, at least to passerine migrants.

If these criteria are valid they will enable us to segregate true, physiological migrants—those individuals whose physiological state is altered preceding migration—from artificial migrants—those individuals which merely wander or are never recovered, and whose banding history has led us to classify them as migrants.

An additional problem which needs clarification is the fact that individuals have been reported which change status from year to year or as they grow older. According to our findings, and the resulting concept of migration as behavior which depends upon a complex, time-consuming series of physiological changes for its expression, it is difficult to imagine how an individual which has inherited a migratory status (behavioristically and physiologically) can alter its status so haphazardly. Perhaps a re-examination of the problem, employing additional criteria for the determination of true migrants, will lead toward a better understanding.

Finally, I canot agree with the implications of the statement by Nice (1937) that a decided rise in temperature in late February will strongly stimulate some male song sparrows to migrate, or similar statements which imply that migration is regulated by weather. I think that weather influences migration only as it would influence the ease, speed, and occurrence of locomotion through the air, or affect the general health or metabolism of the bird. Only when the nervous control of migratory behavior has been released can the weather influence the initiation or continuance of the migratory flight. Also, when the internal stimulus induces the migratory flight, bad flying weather will not necessarily prevent migration, even though the cost in bird lives may be great. The Oregon Junco which was induced experimentally to migrate at the end of January and which was recaptured 10 days later at Redding, California, "flew through" heavy and severe rain storms that had brought the rivers of the State to flood level.

SUMMARY

1. From previous studies it had been demonstrated that juncos could be induced to migrate two months earlier than usual by subjecting them to artificial increases in day length. Migrants which were retained two months past the normal time of departure migrated upon release even though their gonads were in breeding condition. The gonadial cycle differed among residents and migrants under identical environmental or experimental conditions.

2. A group of migrant juncos that was detained at Berkeley through the summer showed that the inhibition of two phases of the annual cycle—the northward migration and breeding—and retention on the wintering grounds did not prevent the occurrence of the normal, subsequent phases of gonadial regression, molt, and preparation for the fall migration as evidenced by a heavy deposition of fat.

3. Two experiments were performed to induce gonadial recrudescence in the fall in White-crowned Sparrows and Oregon Juncos. The lack of any gonadial response in the Oregon Junco indicates that there may be a refractory period in this species. The White-crowned Sparrows respond well to the increases in day length as indicated

by the recrudescence of the gonads, the assumption of fat, and the onset of the prenuptial molt; the resident and migratory races showed differences in gonadial growth and fat deposition comparable to those in the juncos in the induced migration experiments.

4. A cytological study of the anterior lobe of the pituitary revealed that the cells are actively secreting when the testes are recrudescing and when they are at breeding size. When the testes are at winter minimum, the cells are not actively secreting. The estimation of the secretory activity of the cell is based on a study of the Golgi apparatus.

5. Experiments involving the injections of hormones demonstrated that the gonads of juncos will respond to high doses of the gonadotropic and other hormones of the pituitary and to pregnant mare serum. The males respond more readily than do the females. Of the hormones injected, only Antuitrin G (growth hormone primarily plus small amounts of gonadotropic, thyrotropic, and other hormones) induced a physiological state comparable with that which occurs normally preceding migration.

6. Fat deposition during the winter can be segregated into four classes: none, little, medium and heavy. The average body weights of individuals in these classes have been determined.

7. The maximum weight for the species studied occurs immediately preceding the spring migration. This maximum body weight is diagnostic of a readiness to migrate.

8. Resident species studied do not show variations in weight comparable to those in migrants.

9. The weight data and conclusions of Nice and of Baldwin and Kendeigh are contradictory to those here presented, but an analysis reveals that their data are not comparable since they did not segregate the weights of migrants and residents.

10. The stimulus for migration is not one which can be produced suddenly by momentary or transitory variations in the natural environment. Rather, the stimulus results from the physiological response (internal factor) of the bird to regular changes in day length (external factor) over a long period of time.

11. The physiological response is manifested by the growth of the testes, the increase in the secretory activity of the pituitary gland, the heavy deposition of fat, and the concomitant increase in body weight to a maximum.

12. The physiological response of the bird eventually reaches a state that will enable the bird to meet the energy requirements of migration. Then, the behavior patterns which initiate the migratory flight are released.

13. The cyclic nature of the secretory activity of the endocrine system is regarded as an inherent rhythm, since it is a result of the heritable properties of the glandular tissues. The inherent rhythm, however, is not regarded as being automatic or spontaneous, but is under the direct influence of the external environment in a causal relationship.

14. To analyze the problem of individual migration or partial migration in any species it is recommended that physiological migrants and "artificial migrants" be distinguished, using the criteria of banding record, fat deposition, body weight, and reproductive cycle.

LITERATURE CITED

Baldwin, S. P., and Kendeigh, S. C.
1938. Variations in the weight of birds. Auk, 55:416-467.

Baumgartner, A. M.
1938. Seasonal variations in the tree sparrow. Auk, 55:603-613.

Bissonnette, T. H.
1937. Photoperiodicity in birds. Wilson Bull., 49:241-270.

Blanchard, B. D.

1941. The white-crowned sparrows (Zonotrichia leucophrys) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool., 46:1-178.

Bourne, G.

1942. Mitochondria and the Golgi apparatus. Chap. 6 in Cytology and Cell Physiology, ed. by G. Bourne (Oxford, Clarendon Press), xii + 296 pp.

Bullough, W. S.

1942. The reproductive cycles of the British and continental races of the starling. Philos. Trans. Royal Soc. London, Ser. B, 231:165-246.

Groebbels, F.

1932. Der Vogel (Berlin, Gebrüder Bornstraeger), vol. 1:1-918.

Heydweiller, A.

1935. A comparison of winter and summer territories and seasonal variations of the tree sparrow (Spizella a. arborea). Bird-Banding, 6:1-11.

Hirsch, G. C.

1939. Form und Stoffwechsel der Golgi-Körper. Protoplasma Monographs, 18:1-394.

Kirkman, H., and Severinghaus, A. E.

1938. A review of the Golgi apparatus. Parts I, II and III. Anat. Rec., 70:413-431; 557-573; 71:79-103.

Koneff, A. A.

1939. Pituitary changes in male rats reared and maintained on 'pure' dietaries with and without vitamin E. Anat. Rec., 74:383-399.

Linsdale, J. M., and Sumner, E. L., Sr.

1934*a*. Variability in weight in the golden-crowned sparrow. Univ. Calif. Publ. Zool., 40:309-320.

1934*b*. Winter weights of golden-crowned and fox sparrows. Condor, 36:107-112.

1937. Weights of spotted towhees. Condor, 39:162-163.

Lyman, C. P.

1942. Toxic effect of adrenalin on young pigeons. Auk, 59:323-325.

Merkel, F. W.

1938. Zur physiologie der Zugunruhe bei Vogeln. Ber. Ver. Schles. Ornith., 23:1-72.

Miller, A. H.

1941. Speciation in the avian genus Junco. Univ. Calif. Publ. Zool., 44:173-434.

Nice, M. M.

1937. Studies in the life history of the song sparrow. I. Trans. Linn. Soc. N. Y., 4:1-247.

1938. The biological significance of bird weights. Bird-Banding, 9:1-11.

1939. [Review of Merkel, 1938] Bird-Banding, 10:45.

Niethammer, G.

1937. Handbuch der Deutschen Vogelkunde (Leipzig, Akademische Verlagsgesellschaft), 474 pp.

Partin, J. L.

1933. A year's study of house finch weights. Condor, 35:60-63.

Payne, F.

1942. The cytology of the anterior pituitary of the fowl. Biol. Bull., 82:79-111.

Perry, J. C.

1941*a*. The antagonistic action of adrenalin on the reproductive cycle of the English sparrow, *Passer domesticus* (Linnaeus). Anat. Rec., 79:57-77.

1941*b*. Gonad response of male rats to experimental hyperadrenalism. Endocrinology, 29:592-595.

Reese, J. D., Koneff, A. A., and Akimoto, M. B.

1939. Anterior pituitary changes following adrenalectomy in the rat. Anat. Rec., 75:373-403.

Riley, G. M.

1936. Light regulation of sexual activity in the male sparrow (*Passer domesticus*). Proc. Soc. Exp. Biol. Med., 34:331-332.

Rowan, W.

1929. Experiments in bird migration. I. Manipulation of the reproductive cycle: seasonal histological changes in the gonads. Proc. Boston Soc. Nat. Hist., 39:151-208.

1932. Experiments in bird migration. III. The effects of artificial light, castration and certain extracts on the autumn movements of the American crow (*Corvus brachyrhynchos*). Proc. Nat. Acad. Sci., 18:639-654.

Severinghaus, A. E.
1932. A cytological technique for the study of the anterior lobe of the hypophysis. Anat. Rec., 53:1-5.
1933. A cytological study of the anterior pituitary of the rat with special reference to the Golgi apparatus and to cell relationship. Anat. Rec., 57:149-175 .
1937. Cellular changes in the anterior hypophysis with special reference to its secretory activities. Physiol. Rev., 17:556-588.
Schooley, J. P., and Riddle, O.
1938. The morphological basis of pituitary function in pigeons. Amer. Jour. Anat., 62:313-349.
Shaw, T. H.
1935. Variation in the body weight of the tree sparrow, *Passer montanus saturatus* Stejneger. Bull. Fan Mem. Inst. Biol. Peiping, 6:65-69.
Wolfson, A.
1940. A preliminary report on some experiments on bird migration. Condor, 42:93-99.
1941. Light versus activity in the regulation of the sexual cycles of birds: the role of the hypothalamus. Condor, 43:126-136.
1942. Regulation of spring migration in juncos. Condor, 44:237-263.
Zedlitz, O. G.
1926. Vogelgewichte als Hilfsmittel für die biologische Forschung. Jour. f. Ornith., 74:296-308.

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