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REGULATION OF SPRING MIGRATION IN JUNCOS

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Prior to 1925 information concerning the nature of the annual stimulus that induces bird migration was gained primarily from observations made under natural conditions and from banding. The limitations of these methods led to speculations none of which offered a satisfactory exposition of the mechanism involved. Within recent years experimental procedure has been utilized as a new approach to this problem, and the results of this work, when combined with those of the earlier studies, show promise of bringing us closer to a solution.

The impetus for the use of the experimental method in analyzing migration was provided by the results of a series of experiments performed by Rowan (1929). He found that if juncos were subjected to artificial increases in day length in the fall and winter their gonads would recrudesce. With this means of controlling the size of the gonads, Rowan conducted several experiments in migration. They were performed over a period of years and involved the releasing of birds with their gonads at various stages of development. From the results obtained he concluded that migration is controlled by the gonads and hence is a part of the breeding cycle. When the gonads are at winter minimum or spring maximum, there is no inclination to migrate. The stimulus for migration is present, however, when the gonads are recrudescing (spring) or regressing (fall) in response to changes in day length, because of the secretion of the interstitial cells which occur abundantly only during these phases. Later work with castrated crows led Rowan (1932) to conclude that the autumnal migration is independent of the influence of the gonads.

In addition he attempted to show how the increase in day length induces gonadial growth. He substituted compulsory exercise for the artificial light and concluded that light was important only in so far as it enabled the birds to exercise and that this daily increase in activity was the factor which induced gonadial recrudescence.

Since Rowan's initial work (1929) there has been experimentation in many laboratories on the relation of day length to breeding cycles in all the classes of vertebrates. The gonadial cycles have been successfully manipulated in many species, but no corroborative data have appeared for Rowan's "exercise theory." Instead, the theory that light itself is the real factor involved has been promulgated, and although it is accepted by most students of the subject, the evidence for it is confusing and contradictory, and the problem of how the increases in day length induce gonadial growth is still basically unsolved.

Similarly, no corroborative data have appeared for Rowan's theory of migration. The results of the only comparable studies (Wolfson, 1940) are not in agreement with his.

The present work was undertaken to aid in elucidation of these two basic problems —the determination of the annual external and internal stimuli which induce migratory behavior, and the mechanism whereby the external factors effect developmental changes

in the gonads. To accomplish this end, treated birds were released, and the results analyzed in terms of the functions of the gonads, the pituitary, and the hypothalamus. In addition, a careful survey was made of the evidence in support of each of the two theories concerning the mechanism whereby the increases in day length induce gonadial growth. In the light of this survey and our current knowledge of the functions of the hypothalamus and its relation to the pituitary, a new interpretation of the valid evidence can be offered (Wolfson, 1941) which embraces both theories.

In this paper the experiments in migration and the histological studies of the gonads are presented. Results of studies on the pituitary and of some related experiments will be described in later publications.

I wish to express my appreciation to Dr. Alden H. Miller for his material assistance, stimulating counsel, and encouragement during the execution of this work. I am also indebted to the staff of the Museum of Vertebrate Zoology and to the Department of Zoology of the University of California for making available the necessary equipment and laboratory facilities, and to Dr. L. W. Taylor for his coöperation in arranging facilities for captive birds. Much of the research was conducted while the author held the Abraham Rosenberg Research Fellowship in Zoology.

EXPERIMENTS IN MIGRATION

Two types of experiments were performed: induced migration and delayed migration. The species used for all experiments was the Oregon Junco (*Junco oreganus*), a type found commonly on the Pacific coast and in the interior of western North America. It was chosen for several reasons. First, and foremost, both resident and migratory races are contained in the species. Second, it is closely related to the species that Rowan employed and, therefore, the results can be compared with greater validity. Third, both migrants and residents occur in numbers in mixed flocks, are usually easy to trap, and thrive in captivity. Several Slate-colored Juncos (*Junco hyemalis*), which occur rarely in the flocks, also were used.

Miller's (1941) recent studies on speciation in the genus *Junco* provided detailed information on the taxonomy, distribution, and relationships of the members of the *oreganus* group. Without this information it would have been difficult to interpret accurately the results of the experiments.

The migratory races which occur at Berkeley, California, where the experiments were performed, are *J. o. thurberi, J. o. shufeldti, J. o. montanus,* and *J. o. oreganus.*

The breeding range of the members of *thurberi* which winter at Berkeley comprises the Transition and Boreal forests of the coastal districts and the Sierran-Cascade Mountain system in California, north and east of San Francisco Bay. *Shufeldti* breeds in the coastal regions of southern British Columbia, Washington, and Oregon, and intergrades directly with *thurberi.* Populations of *montanus* occur in eastern Oregon, eastern Washington, interior southern British Columbia, northern and eastern Montana, and northwestern Idaho. *Oreganus* is the most northern of the races breeding in the humid coast belt; it occurs in summer from Queen Charlotte Sound, British Columbia, to Yakutat Bay, Alaska.

The two races of *J. hyemalis* which were used are *J. h. hyemalis* and *J. h. cismontanus.* The breeding range of *J. h. hyemalis* extends from the arctic coast of Alaska to New England. The migrants which reach Berkeley probably come from western Canada or Alaska. *J. h. cismontanus* breeds in the interior of northern British Columbia.

Berkeley is at the northern limit of the range of the resident race, *J. o. pinosus.* This form extends southward from the San Francisco Bay region along the coast through Monterey and San Benito counties to San Luis Obispo County.

INDUCED MIGRATION

The purpose of these experiments was to induce a northward migration in winter, two months earlier than the normal time of migration at the end of March. The plan was to subject the experimental birds to artificially increased day lengths during December and January, release them, with the controls, when they were ready to migrate, and record the subsequent behavior by means of trapping and field observations.

Experiment 1.—The first experiment was performed in the winter of 1938-1939. The birds were trapped in October, November, and early December at the poultry ranch in Strawberry Canyon on the campus of the University of California. From here they were taken to the Museum of Vertebrate Zoology where they were banded, identified to race by comparing them with series of skins, and housed indoors for several days. Any individual which could not be identified beyond doubt as a resident or migrant was released. After the birds were accustomed to captivity, they were taken

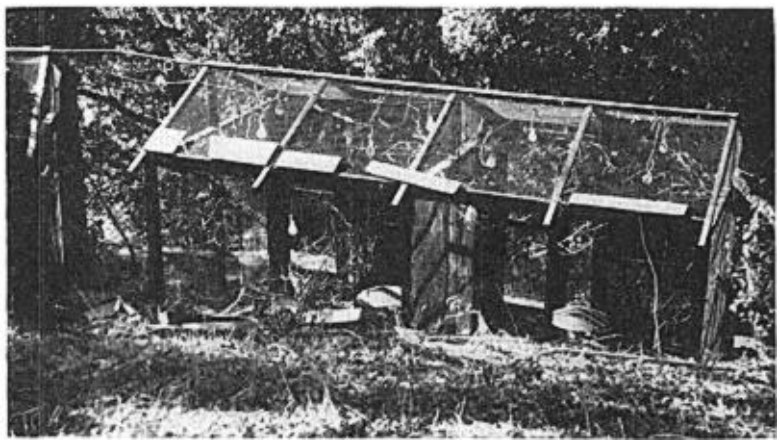

Fig. 79. Outdoor aviary used in experiments with the Oregon Junco in Strawberry Canyon, Berkeley.

to the experimental outdoor cages situated near the trapping stations. Two groups of cages, about five feet apart, were utilized. One group (fig. 79) comprises two adjacent cages, the other three, only two of which were used. The cages are approximately 8′ x 8′ x 8′ and each contains a four-walled house for shelter in inclement weather. The two experimental cages were equipped with two tiers of lights of four bulbs each. They were placed to illuminate all parts of the cage about equally and to prevent shadows and dark corners in which the birds might roost. Two cages in the group of three were used for the controls and were sufficiently blacked out to allow the birds to roost normally.

In spite of the large size of the cages only 16 to 20 juncos were placed in each in order to prevent crowding and to allow sufficient flying space. It was imperative that the birds be in good health. The basic diet was unmixed Argentine canary seed which was kept in sheltered, automatic feeders of one gallon capacity and was renewed when needed to insure an adequate supply. Occasionally humus and freshly cut grass were strewn on the floors of the cages. The juncos also received some insect food, for the cages were situated in a live oak-California bay habitat. On many occasions juncos were seen capturing moths and other flying insects which were attracted to the lights at

night. There was always a supply of water for drinking and bathing. Indicative of the successful handling of the birds was a low mortality.

On December 12, 1938, the day length was increased one hour, one-half hour each at sunset and sunrise. The normal day length at Berkeley on this date is approximately 9 hours and 40 minutes, only 5 minutes longer than the shortest day of the year. Thereafter the day length was increased automatically about 3 minutes a day, the increments being added partly in the morning and partly in the evening. On February 7, 1939, when the juncos were released, the day length for the experimentals was 13 hours and 30 minutes, for the controls 10 hours and 30 minutes.

Samples were taken during the experiment to determine when the experimentals had reached an internal state similar to that which occurs at the normal time of migration. The gonads were fixed in Bouin's fluid and measured after fixation with dial calipers calibrated to tenths of a millimeter. The anteroposterior and the transverse dimensions of the testes were taken as they lay on the dorsal body wall. The fat condition of each bird, an important indicator of a bird's readiness to migrate, was estimated and recorded in four classes: no fat, little fat, medium fat, and heavy fat. Occasionally plus and minus were used to indicate extremes. These classes denote not only the amount of fat present, but also its distribution. In a bird with "no fat" the furculum and pterylae are practically clean. In a bird with "little fat" there are small amounts on these parts. In the "medium" class, fat occurs in good amounts along the pterylae, fills the crotch of the furculum and begins to appear in the axilla, on the flanks, sides of the neck, lower back, and abdomen. In a bird with "heavy fat" the amounts are increased in all of the aforementioned locations, especially the abdomen and lower back. The abdomen bulges with fat due to the intraperitoneal deposition, in addition to the subcutaneous, and the yellow color is readily visible through the skin. These classes are similar to those which Blanchard (1941) has used in describing the fat condition of the White-crowned Sparrow (*Zonotrichia leucophrys*). However, there is a difference in terminology in two classes; our "heavy" and "heavy +" classes are equivalent to her "fat" and "very fat" categories, respectively.

A summary of the samples taken prior to the date of release is given in table 1. The

TABLE 1

Samples taken in 1939 before release of February 7

Date	Sample no.	Band	Sex	Race*	Testis size mm.	Testis volume, mm.³	Body weight, gm.	Fat
				Experimentals				
Jan. 4	2	139-5738	♂	T	L-1.1x1.0	.57	.....	None
					R-1.1x1.0	.57	.....	
Jan. 16	27	38-17464	♀	T			16.0	Medium
Jan. 26	7	139-5771	♂	S	L-1.4x1.1	.88	15.5	None
					R-1.2x1.2	.90		
Feb. 5	5	139-5763	♂	T	L-2.2x1.6	2.56	19.0	Heavy+
					R-1.9x1.7	2.88		
				Controls				
Jan. 4	3	139-5714	♂	T	L-1.0x0.7	.25	.....	None
					R-0.9x0.8	.30		
Feb. 5	15	139-5707	♂	S	L-1.2x0.9	.51	17.0	Little
					R-1.2x0.8	.40		
Feb. 5	37	.....	♂	S	L-.....		14.7	None
					R-0.9x0.8	.30		

* Subspecies are abbreviated in tables as follows. Migrants: T=*thurberi*; S=*shufeldti*; M=*montanus*; O=*oreganus*; C=*cismontanus*; H=*hyemalis*. Resident: P=*pinosus*.

controls had normal gonads for February 5, while the gonads of the experimentals were well advanced and equivalent to those of birds taken in late March when migration normally occurs. The "heavy fat" condition of the experimentals, in addition to the enlarged testes, is diagnostic of a readiness to migrate. At the normal time of migration the testes range in total volume (left plus right) from 2.0 mm.^{3} to 4.5 mm.^{3}, and the birds have a heavy or medium deposition of fat.

Prior to release the birds were banded with combinations of colored bands for the identification of individuals, and small curved chicken feathers, which were dyed various colors to indicate residents and migrants, experimentals and controls, were attached to the bases of the middle rectrices with Duco cement. With the aid of these colored feathers the behavior of the resident and migratory races after release could be recorded and the birds could be easily found in the field. The feathers did not interfere with the flight of the bird, nor did they prevent the spreading of the tail. The birds were well accustomed to them within a few hours and I did not observe any changes in behavior attributable to them.

On February 7, 26 experimentals and 19 controls were released. The numbers of each sex and subspecies are given in table 2. One of the experimental migrants, a male *oreganus,* had been used in an earlier experiment in 1938 and had returned to the trapping station after the breeding season. It was familiar, therefore, with the immediate vicinity and had exhibited a strong "homing instinct."

The doors of the cages were opened at 2:55 p.m. and within a period of 5 minutes most of the birds were in the California bay tree adjacent to the cages. I chased out the remainder of the birds. Several minutes later I observed the majority of the group feeding in the live oaks about 25 yards west of the cages. They appeared to be in a

TABLE 2

Birds released and retrapped in Experiment 1

	Experimentals				Controls			
	♂		♀		♂		♀	
	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.	Ret.	Ret.
Migrants								
thurberi	5	3	1	1	4	4	5	5
shufeldti	1	1	8	5	1	1	1	1
montanus	....	....	1	1	....	....	1	1
oreganus	2	0	1	0	2	1	2	2
Totals	8	4	11	7	7	6	9	9
Per cent retaken		50		64		86		100
Residents								
pinosus	2	2	5	4	1	1	2	2
Per cent retaken		100		80		100		100

loose flock. Until 3:10 p.m. it had been raining lightly. The sky was overcast and a strong wind was blowing from the northwest. Then the rain abated, and it became brighter on the ground. A *pinosus* was singing while the flock was in the oak trees. When it became brighter, the birds dropped to the ground to continue their feeding. The flock became more compact and seemed identical to other winter flocks in form and behavior. There was no fighting, chasing, or evidence of breeding behavior. Migrants and residents, experimentals and controls were together, and they foraged as close to each other as individuals in a normal flock. The singing of the *pinosus* became more regular during this period of feeding on the ground. Six full songs were given in 10 minutes. Wild *pinosus* were not yet singing regularly at Berkeley. I approached closer to the birds and flushed them. They flew as a flock, 2 to 3 birds starting first and the

rest following, to a point about 50 yards eastward where they began feeding again. I repeated this procedure several times to confirm the flocking behavior.

At 4:00 p.m. it began to rain again and the wind became stronger. I left the large flock about 200 yards east of the cages and found a near-by group of 6 juncos by following the song of the *pinosus*. I returned to the cages and near-by trapping stations where seed had been placed and observed 2 birds, both of them in the cages. The doors of the cages had been left open and food and water were available. About 4:30 p.m., the large flock appeared at the trapping station 30 yards north of the cages. It was still raining and the attached chicken feathers had contracted to thin lines. At 5:00 p.m. when I left the canyon, these birds were still feeding.

The significant points in these observations follow: (1) In spite of the fact that the birds were in different physiological states, within 15 minutes after they were free they were in a compact flock. (2) During the first two hours of their freedom the birds moved in an approximate circle within an average radius of 100 yards from the cages. (3) They remembered and returned to the trapping stations where many of them had been caught two to three months earlier. (4) The singing of the *pinosus* (and courtship behavior observed later) was definitely in advance of the season and indicated a difference between the migrants and residents in the response to the experimental treatment.

During the next few days trips were made regularly to the canyon. The juncos were observed at the trapping stations and around the cages. They were in well formed flocks which included wild juncos. Exceptions were two *pinosus*, a male and female, which were paired. They kept together, were not seen in any flock, and exhibited weak courtship behavior. Individuals were recorded by means of the colored band combinations and trapping. Any trapped juncos were released immediately. The plan was to allow several days for the birds to become accustomed to their freedom before they were retrapped and sampled. On February 12, five days after the release, the first samples were taken. The next large group was taken on February 15, after which date trapping became irregular. These samples are listed in table 3.

TABLE 3

Samples taken in 1939 after release of February 7

Experimentals

Date	Sample no.	Band	Sex	Race	Testis size mm.	Testis volume, mm.³	Body weight, gm.	Fat
Feb. 12	4	139-5760	♀	P			16.0	None
Feb. 12	8	139-5751	♀	P			15.5	None
Feb. 12	9	139-5774	♂	S	L-1.4x1.1	.88	17.5	Little
					R-1.4x1.1	.88		
Feb. 15	41	139-5791	♂	P	L-8.1x6.2	163.1	18.2	None
					R-6.9x6.3	143.4		
Feb. 15	46	139-5773	♂	T	L-1.7x1.2	1.29	17.5	Medium—
					R-1.5x1.2	1.13		
Feb. 15	47	139-5796	♂	P	L-6.4x4.5	67.9	16.7	None
					R-5.7x5.0	74.5		
Feb. 15	48	139-5740	♀	T			16.8	Medium
Feb. 15	49	139-5749	♀	S			17.4	Medium+
Feb. 15	50	139-5789	♀	P			14.5	None
Feb. 15	52	139-5770	♀	S			16.2	Little
Feb. 15	54	139-5745	♀	M			19.7	Heavy
Mar. 16	62	139-5793	♀	S			17.2	Medium
Mar. 16	64	139-5756	♂	T	L-1.4x1.1	.88	17.2	Medium
					R.....			
Mar. 20	79	139-5746	♀	P			15.1	None
Mar. 23	86	139-5733	♂	T	L-1.7x1.3	1.51	18.5	Heavy+
					R-1.6x1.4	1.64		

Controls

Date	Sample no.	Band	Sex	Race	Testis size mm.	Testis volume, mm.³	Body weight, gm.	Fat
Feb. 12	13	138-5757	♂	O	L-1.1x1.8	.37	20.8	Medium+
					R-0.9x0.8	.30		
Feb. 12	16	139-5797	♂	T	L-0.7x0.6	.13	17.3	Medium
					R-0.6x0.6	.13		
Feb. 12	17	139-5788	♀	P			16.6	None
Feb. 12	26	139-5711	♀	T			19.5	Medium+
Feb. 12	36	139-5723	♂	S	L-0.9x0.6	.16	17.3	Medium
					R-0.9x0.7	.23		
Feb. 15	38	139-5715	♂	P	L-1.8x1.5	2.12	16.6	
					R-1.7x1.5	2.00		Medium
Feb. 15	40	139-5702	♂	T	L-1.0x0.7	.25	17.2	
					R-0.9x0.8	.30		Medium
Feb. 15	42	139-5701	♂	T	L-1.0x0.7	.25	17.1	
					R-1.0x0.8	.33		Little
Feb. 15	45	139-5705	♂	T	L-1.0x0.8	.33	16.5	
					R-0.9x0.7	.23		None
Feb. 15	51	38-31507	♀	S			16.5	Medium
Feb. 15	53	139-5716	♀	T			16.2	Medium

The purpose of sampling the retrapped birds was to determine their readiness for migration by recording the condition of the gonads, the fat, and the general health. A study of table 3 reveals that the experimental juncos that were retrapped in February were not ready to migrate, even though the gonads were enlarged, because of an inadequate amount of stored fat. One possible exception is sample number 54, a female *montanus*. Apparently the day length schedule was not correct for a uniform response among the migrants. A *thurberi* that was sampled before the release was definitely ready to migrate, and some of the experimental migrants must have responded equivalently, for not all of them were retrapped.

The numbers and kinds of juncos which remained are recorded in table 2. In a few instances the records are from field observations and not from trapping, but these are included in the table as retraps when it is definitely known that the birds failed to migrate. A complete history of the birds that were retrapped soon after release and those that repeated frequently in subsequent winters is on file at the Museum of Vertebrate Zoology. It is noteworthy that the males responded to the light treatment better than the females. The probability that they undertook a northward migration will be discussed later. The almost complete retrapping of the controls and residents emphasizes the significance of the failure to retrap all of the experimental migrants.

The apparent deficiencies in this experiment were an insufficient number of males, particularly of the more northern races, and an inadequate day length schedule, due to the too small daily increases and an insufficient total day length at the end of the experiment. To rectify these deficiencies and obtain more conclusive evidence the experiment was repeated in the winter of 1939-1940.

Experiment 2.—The main differences in method in this experiment were the day length schedule and the increased number of birds that was released.

The experiment was begun on December 10 when the normal day length was 9 hours and 40 minutes. On that day the day length was increased one hour and 30 minutes, making a total day length of 11 hours and 10 minutes. Thereafter, the day length was increased about 10 minutes every two days, equal increments being added before sunrise and after sunset. On the day of release, January 31, the experimental day length was 15 hours and 30 minutes, the normal day length, 10 hours and 15 minutes. Dis-

counting the initial increase, the average daily increase was about 5 minutes for the 51 days, as compared with a daily increase of about 3 minutes for the 57 days in experiment 1. In experiment 1, the daily increases were controlled automatically by an astronomical dial on a time clock; the clock was set at the start only. In this experiment and the one following, the daily lighting was still controlled by the time clock, but the clock had to be set every two days for the desired increment.

To provide for an increased number of experimentals, the control cage nearest to the experimental group was equipped with lights. The remaining control cage was well protected from the artificial light, but it could not be blacked out completely.

The samples taken prior to release are listed in table 4. The lighting schedule was far more effective than before, since the gonads responded more uniformly and were larger than gonads at the normal time of migration. The difference in response between the residents and migrants is clearly indicated by the gonad sizes and fat condition. Samples 162, 163, 179, and 180 show low weights because of intestinal parasites and internal injuries.

On January 31, 53 experimentals and 23 controls were released. Three residents and three migrants had repeated at the trapping stations before they were retained for this experiment, and were, therefore, familiar with the grounds of the poultry ranch. The number of each sex and subspecies is given in table 5. To insure the correct date for release, the fat condition of each bird was examined when it was "feathered" and "color-banded" by blowing on the feathers and exposing the apteria. The amount and distribution of the yellow fat was easily estimated. Of the 43 experimental migrants that were released only 7 did not show a "heavy fat" deposition. The controls showed "no fat" or "little fat."

TABLE 4

Samples taken in 1940 before release of January 31

Date	Sample no.	Band	Sex	Race	Testis size mm.	Testis volume, mm.^{3}	Body weight, gm.	Fat
Experimentals								
Jan. 12	153	39-61131	♂	O	L-2.0x1.5	2.36	19.7	Heavy—
					R-1.9x1.5	2.24		
Jan. 14	154a	39-61060	♀	P			.....	None
Jan. 18	162	39-61107	♂	S	L-1.8x1.2	1.36	13.3	None
					R-1.6x1.2	1.21		
Jan. 23	163	39-61071	♂	T	L-1.8x1.1	1.14	13.4	None
					R-1.5x1.2	1.13		
Jan. 26	164	39-61062	♂	P	L-6.4x4.8	77.4	18.5	Medium—
					R-5.5x5.3	80.9		
Jan. 26	165	39-61118	♂	P	L-3.1x2.4	9.38	15.6	Little
					R-2.8x2.3	7.76		
Jan. 26	166	.....	♂	P	L-2.0x1.6	2.68	16.9	None
					R-2.0x1.6	2.68		
Jan. 26	167	39-61059	♀	S			16.6	Little
Jan. 27	168	39-61125	♂	S	L-2.6x2.1	6.00	22.6	Heavy+
					R-2.5x2.1	5.77		
Jan. 27	169	39-61103	♀	T			19.0	Heavy
Jan. 27	177	39-61136	♂	P	L-5.3x4.5	56.2	17.9	Little
					R-4.3x4.1	38.0		
Controls								
Jan. 30	178	39-61146	♂	P	L-1.3x0.9	.55	14.8	None
					R-1.1x1.1	.63		
Jan. 30	179	39-61139	♀	S			11.7	None
Jan. 30	180	39-61152	♀	T			12.6	None

The doors of the cages were open at 10:00 a.m. After waiting ten minutes and not seeing any juncos fly out, I drove all of them from the cages in about three minutes. They flew into the bay and live oak trees over the cages. For a few minutes there was no foraging or singing. The birds were perched quietly, and there were several attempts at preening. Then there was an occasional song and some controls and residents came to the ground to feed. Although the sky was overcast, it was bright. After a half an hour I noticed that there were only a few controls and residents about the cages, but no experimental migrants. I left the vicinity of the cages and started north to the trapping stations. Two hundred yards west of a trapping station was a large, loose flock of experimentals feeding in the moist grass. The yellow marker feathers stood out well. Not one control bird was in this flock of 40 experimental migrants and residents.

During the next hour the flock continued foraging in this location. There were at least two instances of sexual chasing, involving both the residents and migrants. Song was given occasionally. I left the canyon at 12:30 p.m. and returned at 2:30 p.m. I found the controls and some experimentals around the cages and identified experimental migrants and experimental residents singing. Activity became more pronounced that afternoon, with abundant singing and definite and frequent chasing. Two experimental residents seemed to be paired. They followed each other, and there was singing and chasing. I left the vicinity of the cages and found the large flock again at the same

TABLE 5

Birds released and retrapped in Experiment 2

	Experimentals				Controls			
	♂		♀		♂		♀	
	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.	Ret.	Ret.
Migrants								
thurberi	9	1	7	5	5	5	8	7
shufeldti	12	1	6	2	2	2	2	2
montanus	1	0	2	0	....	....	....	....
oreganus	5	0	....	....	2	1	....	....
cismontanus	....	....	1	0	....	....	....	....
Totals	27	2	16	7	9	8	10	9
Per cent retaken		7		44		89		90
Residents								
pinosus	7	5	3	1	4	4	....	....
Per cent retaken		71		33		100		

place. The flock, which now included 2 controls, moved northward gradually about 300 yards, foraging on the ground occasionally for short periods. It then moved south again over the same ground it had just covered. When I left the canyon at 4:30 p.m., the flock was foraging where it was first discovered.

On February 1, I returned to the canyon at 8:00 a.m. Singing was common in the experimental migrants and residents, whereas no control was ever heard singing. The experimentals were less numerous and the large flock of the day before could not be found. The controls and experimentals that were observed were in the vicinity of the cages. On February 2 the traps were set and 13 birds were caught and sampled. On February 3 several controls and residents were seen in the vicinity of the cages. Traps were set again on February 4 and two experimentals were caught and sampled. The two experimental *pinosus* seen earlier were still paired. The male was sampled on February 5 and had testes of breeding size. From this date on regular visits were made to the canyon and the individuals found were recorded. No further samples were taken until March when two experimentals were discovered and trapped.

The significant points in these observations are the flocking behavior, the restriction of foraging to an area near the cages and the trapping stations, and the difference in behavior of experimental residents and migrants as exemplified by pairing. These points are in agreement with the behavior in experiment 1.

The samples taken after the release are listed in table 6. Several points are worth noting. (1) Only two experimental migrant males were retaken. (2) The study of the fat condition of the experimental migrants prior to release showed that 7 birds did not have a heavy deposition of fat. All of these birds were retrapped, and are included in the table; one bird, number 204, had reached the "heavy fat" class, although it was released only four days before with little fat. Its gonads were also much advanced over the other migrant samples. This storage of abundant fat in four days indicates that a definite physiological change is produced by the experimental treatment which persists even after the treatment lapses. This bird may not have been able to get a sufficient amount of proper food in captivity because of the definite social hierarchies which are formed in the cages. (3) Only one retrap, number 205, was definitely ready to migrate but did not. Might its failure to migrate be due to the fact that it was not part of a

TABLE 6

Samples taken in 1940 after release of January 31

Date	Sample no.	Band	Sex	Race	Testis size mm.	Testis volume, mm.^{3}	Body weight, gm.	Fat
				Experimentals				
Feb. 2	181	39-61115	♀	T			16.5	Little
Feb. 2	183	39-61110	♀	S			17.4	Medium
Feb. 2	184	39-61075	♂	P	L-7.0x5.7	118.8	15.9	None
					R-6.9x6.0	130.0		
Feb. 2	185	39-61082	♀	T			14.9	Little—
Feb. 2	190	39-61038	♂	P	L-7.8x5.2	110.5	16.1	None
					R-6.6x6.1	128.7		
Feb. 2	191	39-61083	♀	T			16.2	None
Feb. 2	193	39-61057	♂	S	L-2.4x1.9	4.54	17.6	Little
					R-2.3x2.1	5.32		
Feb. 4	204	39-61065	♂	T	L-4.3x3.5	27.6		Heavy
					R-3.9x3.3	22.2		
Feb. 4	205	39-61073	♀	S			20.0	Heavy
Feb. 5	206	39-61066	♂	P	L-7.3x5.5	115.5	17.2	None
					R-6.1x6.1	118.8		
Mar. 16	212	39-61081	♀	T			17.7	None
Mar. 30	222	39-61050	♀	T			18.4	Little
				Controls				
Feb. 2	182	39-61145	♀	T			16.6	Little
Feb. 2	188	39-61124	♀	T			16.5	Little+
Feb. 2	189	39-61142	♂	T	L-1.2x0.9	.51	17.1	Little
					R-1.2x0.8	.40		
Feb. 2	192	39-61138	♂	P	L-1.3x0.9	.55	16.3	None
					R-1.1x0.9			
Feb. 2	194	39-61156	♂	T	L-1.0x0.8	.33	17.9	Medium
					R-1.1x0.8	.37		
Feb. 2	195	39-61132	♂	T	L-0.9x0.7	.23	16.1	Little—
					R-0.9x0.7	.23		

migrating flock? (4) The fully developed gonads of the *pinosus* stand in marked contrast to the rescrudescing gonads of the migrants. Yet the experimental treatment of migrants and residents was identical.

The numbers of each sex and subspecies that were retaken are listed in table 5. The small number of experimental migrants that was retaken, particularly of males, as

compared to the almost complete retrapping of the controls and residents strongly indicates that the experimentals migrated. Positive proof of the fact that they did migrate, and northward too, was the retaking of an experimental migrant, a female *shufeldti,* at Redding, California, about 200 miles north of Berkeley, on February 10. Judging from the date of capture, the stormy weather which prevailed during the first week in February, and the disappearance of the experimental migrants from Strawberry Canyon after the day of release, I assume that the migrating flock left Berkeley either in the course of the night of January 31, or early on the morning of February 1.

The attached yellow feather was responsible for the record from Redding. The junco was caught by a cat, whose owner was attracted to the unusual appearance of the bird. He discovered the bands and forwarded them to the California Fish and Game Division in San Francisco. They informed the Biological Survey in Washington, and within a few days I was notified of the record. The flight of this bird was along the normal flight line of many migrants, namely through the Sacramento Valley. The lack of interference of the attached feather and bands with the flight of the birds is in some measure confirmed by this record.

As in experiment 1, the males showed the best response. The failure to retrap all of the experimental residents may be explained by the scattering of individuals caused by the activity of the mature gonads. Evidences of mating behavior among the *pinosus,* which were recorded in both experiments, lend support to this view.

In spite of the evidence obtained in this experiment, which proved that juncos could be induced to migrate northward during the winter by subjecting them to increasing day lengths, the experiment was repeated again during the winter of 1940-1941 to obtain additional evidence and to test the conclusions of the previous experiments.

Experiment 3.—One major innovation in method, a more advanced day length schedule, was adopted in an attempt to bring the birds into the migratory state earlier in January.

The experiment was begun on December 10, 1941, and the initial increase in day length was one hour and 35 minutes, making a total day length of 11 hours and 15 minutes. Thereafter until January 15, the day length was increased about 14 minutes every two days, and it was administered as before. From January 15 to January 29, when the juncos were released, the day length was constant at 15 hours and 20 minutes. The average daily increase until January 15 was about 7 minutes. A summary of the lighting schedules for the three experiments is given in table 7. All day lengths are approximated to within two minutes.

TABLE 7

Lighting schedules of induced migration experiments

	Experiment 1 1938-1939	Experiment 2 1939-1940	Experiment 3 1940-1941
Date of Start	December 12, 1938	December 10, 1939	December 10, 1940
Normal day length[1]	9 hrs. 40 min.	9 hrs. 40 min.	9 hrs. 40 min.
Initial increase	1 hr.	1 hr. 30 min.	1 hr. 35 min.
Total day length	10 hrs. 40 min.	11 hrs. 10 min.	11 hrs. 15 min.
Duration of Experiment	57 days	51 days	49 days
Average daily increase[2]	3 min.	5 min.	7 min.[3]
Date of Release	February 7, 1939	January 31, 1940	January 29, 1941
Experimental day length[4]	13 hrs. 30 min.	15 hrs. 30 min.	15 hrs. 20 min.
Normal day length	10 hrs. 30 min.	10 hrs. 15 min.	10 hrs. 10 min.

[1] Normal day length for December 21 is 9 hours and 35 minutes.
[2] Average daily increase from December 21 to April 1 (when migration has begun) is 2 minutes for the 100 days.
[3] Daily increases were administered for 36 consecutive days only.
[4] Day length for April 1 is 12 hours and 35 minutes.

The samples taken before release are given in table 8. The lighting schedule was more effective than in the previous experiments as shown by the gonads and fat condition of the *oreganus* that was sampled on January 11. The difference in gonadial response between residents and migrants is again confirmed by the uniform response of the *pinosus*.

Although many of the birds were ready to migrate by the middle of January, they were held until January 29 to insure a sufficient deposition of fat by the females. On that day 53 experimentals and 10 controls were released. The examination of the fat condition prior to release revealed that the controls and residents had "no fat," and all but 5 of the experimental migrants had a heavy deposition of fat. Three experimentals and one control had previous trapping histories.

The behavior on the day of release was similar to that in the previous experiment with two exceptions: there was more singing, and the flock which formed contained more controls. Because it was felt that the birds were retrapped too soon after the

TABLE 8

Samples taken in 1941 before release of January 29

Date	Sample no.	Band	Sex	Race	Testis size mm.	Testis volume, mm.³	Body weight, gm.	Fat
Experimentals								
Jan. 3	268	140-65129	♀	O			17.9	Medium+
Jan. 4	276	140-65184	♂	T	L-1.7x1.6	2.28	.....	Medium—
					R-1.8x1.5	2.12		
Jan. 11	304	140-65121	♂	O	L-1.8x1.4	1.85	20.9	Heavy+
					R-1.7x1.5	2.00		
Jan. 18	307	140-65179	♂	P	L-3.7x2.9	16.3	16.0	None
					R-3.0x2.7	11.5		
Jan. 18	308	140-65187	♂	P	L-3.9x2.9	17.3	15.4	None
					R-3.5x2.6	12.4		
Jan. 18	309	140-65178	♂	P	L-3.3x2.6	11.7	14.6	Little
					R-2.9x2.6	10.3		
Jan. 18	310	140-65174	♂	P	L-5.1x3.6	35.8	15.8	Little
					R-4.6x4.0	38.5		
Jan. 21	320	140-65185	♀	S			19.0	Heavy+
Jan. 21	321	140-65150	♂	O	L-2.0x1.5	2.68	19.1	Heavy+
					R-1.8x1.7	2.72		
Jan. 23	322	140-65135	♂	P	L-6.3x4.9	79.4	.....	None
					R-5.9x5.1	80.5		
Jan. 29	325	140-65168	♀	P			15.7	None
Control								
Jan. 14	305	.....	♂	S	L-0.9x0.8	.30	15.6	None
					R-0.8x0.8	.27		

release in 1940, no birds were retrapped and sampled until February 13. Until then, however, trips were made to the canyon regularly and a record kept of all observations. Nearly all of the experimental migrants left before January 30, for from that date on no more than three were recorded. The controls and residents were seen regularly. The samples taken after release (see table 10) showed that the migrants which remained had an inadequate fat supply, and their gonads had not responded well. These migrants had only a little fat prior to release. A bird that was released with little fat showed a heavy fat supply when it was retrapped on February 14. It was released and not retrapped again.

That the lighting schedule employed in this experiment was the most effective of any used is shown by table 8. The results substantiate beyond any reasonable doubt the

TABLE 9

Birds released and retrapped in Experiment 3

	Experimentals ♂		♀		Controls ♂		♀	
	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.
Migrants								
thurberi	12	1	1	0	3	3	....	....
shufeldti	3	0	7	0	2	2	2	2
montanus	1	0	2	0	....	....	....	....
oreganus	10	1	2	0	....	....	....	....
Totals	26	2	12	0	5	5	2	2
Per cent retaken		8		0		100		100
Residents								
pinosus	10	5	5	1	2	2	1	1
Per cent retaken		50		20		100		100

TABLE 10

Samples taken in 1941 after release of January 29

Date	Sample no.	Band	Sex	Race	Testis size mm.	Testis volume, mm.³	Body weight, gm.	Fat
				Experimentals				
Feb. 13	338	140-65122	♂	T	L-1.6x1.2	1.21	15.7	None
					R-1.5x1.3	1.33		
Feb. 13	342	140-65163	♂	P	L-3.3x2.3	9.14	16.5	None
					R-3.1x2.3	8.58		
Feb. 13	343	140-65123	♀	P			14.5	None
Feb. 14	350	140-65126	♂	P	L-7.9x5.3	116.1	15.6	None
					R-7.2x5.7	112.6		
Feb. 14	351	140-65171	♂	P	L-6.5x4.5	69.0	16.5	None
					R-5.3x5.0	69.2		
Feb. 14	353	140-65136	♂	P	L-1.9x1.4	1.95	16.3	None
					R-1.7x1.3	1.51		
Mar. 16	B-2	140-65159	♂	O	L-1.2x0.8	.40	17.6	Little
					R-1.0x1.0	.58		
				Controls				
Feb. 13	337	39-61192	♂	S	L-1.1x0.7	.28	16.3	None
					R-1.0x0.7	.26		
Feb. 13	339	38-17436	♂	T	L-1.8x1.3	1.59	18.1	None
					R-1.6x1.3	1.42		
Feb. 13	340	39-61188	♂	T	L-1.2x0.8	.40	16.4	None
					R-0.9x0.8	.30		
Feb. 13	341	39-61193	♂	S	L-1.2x0.8	.40	17.5	Little
					R-1.2x0.9	.51		
Feb. 13	345	39-61189	♀	S			15.8	None
Feb. 14	352	39-61191	♂	P	L-1.9x1.4	1.95	15.5	Little
					R-1.7x1.4	1.74		
Feb. 14	354	140-65177	♀	S			15.1	Little

conclusions and results of the previous experiments. Of the 38 experimental migrants that were released only 2, about 5 per cent, failed to migrate, as compared with 58 per cent in experiment 1, and 20 per cent in experiment 2. The scattering of the experimental *pinosus* was again demonstrated. The controls were retrapped completely despite the small number that was used and their freedom for two weeks. Their extended freedom and recapture lends support to the belief that if the migrants had failed to go north, they would not be several miles away, but they would be in Strawberry Canyon and in the vicinity of the cages.

From the results of these three experiments, I conclude that juncos can be induced to migrate northward during the winter by subjecting them to artificially increased day lengths which will bring them into a physiological state similar to that which prevails at the normal time of migration.

DELAYED MIGRATION

These experiments were undertaken to determine whether juncos would migrate if detained on their wintering grounds and released when their gonads had attained breeding size.

The results of two of these experiments (numbers 4 and 5) have already been reported (Wolfson, 1940). They demonstrated that juncos will migrate as late as sixty days after the normal date of departure even though their gonads are of breeding size. For further corroboration, the experiment was repeated in 1940.

Experiment 6.—Juncos were trapped from December, 1939, through March, 1940, and handled as in the previous experiments in regard to housing, banding, and examination of fat prior to release. No artificial lighting was employed. On June 8, 1940, 26 migrants, 3 of which had previous trapping histories, and 8 residents were released. Only three birds did not show a heavy deposition of fat. The aggressive behavior of the birds after release simulated that in experiment 4, but it was not as lasting. By early afternoon the singing, chasing, and scolding, which were prevalent after the release at 10:00 a.m., had practically ceased.

On June 9 only one migrant and two residents could be found, and they were in the vicinity of the cages. On June 10 these birds were collected (see table 12). The migrant showed only a medium supply of fat, whereas prior to release its fat condition was recorded as "little." The ovaries of all three birds contained well developed follicles and the oviducts were enlarged. During the summer only one marked bird, a male *pinosus* was seen in the canyon, but in the fall and winter three migrants were retrapped. A summary of the numbers of the birds that were released and retrapped in the delayed migration experiments is given in table 11. The results of this experiment further substantiate the previous conclusion.

TABLE 11

Birds released and retrapped in delayed migration experiments

	Experiment 4—1938				Experiment 5—1939				Experiment 6—1940			
	♂		♀		♂		♀		♂		♀	
	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.	Rel.	Ret.
Migrants												
thurberi	4	0	2	0	7	0	8	0	7	0	7	1
shufeldti	9*	0	3	0	5	1	....	....	2	0	2	0
montanus	1	0	1	0	....	....	1	0	....	....	1	0
oreganus	5	0	7	0	4	0	2	0	4	0	2	0
cismontanus	1	0	....	....	....	....	....	....	....	....	....	....
hyemalis	....	....	1	0	....	....	....	....	1	0	....	....
Totals	20	0	14	0	16	1	11	0	14	0	12	1
Per cent retaken		0		0		6		0		0		8
Residents												
pinosus	2	2	3	2	5	2	1	1	4	1	4	2
Per cent retaken		100		67		40		100		25		50

* Sex identification of three of these is questionable.

TABLE 12

Samples taken in Experiment 6—release of June 8, 1940

Date	Sample no.	Band	Sex	Race	Testis size, mm.	Testis volume, mm.^{3}	Body weight, gm.	Fat
Birds not released								
Jun. 4	226	39-61141	♂	T	L-6.0x4.5	63.5	.....	Medium
					R-5.1x4.1	44.7		
Jun. 5	227	39-61178	♀	T			.....	Heavy
Jun. 5	228	38-31507	♀	S			.....	Heavy
Jun. 5	229	39-61045	♀	S			.....	Heavy
Birds released								
Jun. 10	230	39-61171	♀	T			.....	Medium
Jun. 10	231	39-61165	♀	P			.....	Little
Jun. 10	232	39-61155	♀	P			.....	Medium—

HISTOLOGY OF THE GONADS

Oregon Juncos were trapped in the field, or taken from the experimental cages, and were brought into the laboratory alive. They were killed with chloroform or ether, weighed, skinned, and the gonads fixed in Bouin's fluid within ten minutes after death. Both testes were measured after fixation with dial calipers calibrated to tenths of a millimeter. The anteroposterior and the transverse dimensions of the testes were taken as they lay on the dorsal body wall. Dioxane was used for dehydration and paraffin for embedding. Serial sections of the testes were cut sagittally at ten microns, but only the center sections of the larger testes were studied. Previous studies of several complete series had shown that no differences existed at various levels. The sections were stained with Delafield's haematoxylin and eosin. For accuracy in making comparisons of size, the volumes of the left and right testes were computed, and then added to give the total testis volume. The formula for the volume of an ellipsoid $V=4/3\ \pi ab^2$ was used, where a=½ the longest diameter and b=the shortest diameter. From these volumes the most probable growth curve was calculated. The distribution of points fitted best a simple exponential curve of the general formula $V=A\times 10^{Bt}$ where V=volume, t=time, and A and B are constants to be determined from the data. From this formula the most probable volume of a testis collected on a particular date after November 30 could be determined.

As other workers have found, the left testis is longer when there is a difference in length between left and right testes, but upon computing the volumes it was found that in many instances the right testis is larger. This is due to its more nearly spherical shape in contrast to the more ellipsoidal shape of the left testis. Studies of both testes of several individuals showed that there was little or no histologic difference between them, except when the difference in volume was great.

GONADS OF RESIDENT MALES

Gross changes.—The testes reach their minimum size, 0.5 mm.^{3}, in late October, and remain at this size through November and early December. Beginning in the middle of December there is a slight, gradual increase in size with the testes 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 200 mm.^{3} there is a rapid increase in the rate of growth. These changes are indicated in the graphs (figures 80 and 81).

Volume changes and growth rates of equivalent magnitude have been described

for other passerine birds (Loisel, 1900, 1901; Kirschbaum and Ringoen, 1936, for *Passer domesticus;* Watson, 1919, *Ligurinis chloris;* Rowan, 1929, *Junco hyemalis;* Bissonnette, 1930, *Sturnus vulgaris;* Blanchard, 1941, *Zonotrichia leucophrys*).

Histologic changes.—Concomitant with the changes in size are changes in the histologic condition of the testis. These changes have been recorded for the species just mentioned, and they show that size is a reliable index of the histologic condition. Particularly apposite to the present study are the studies of Rowan on the Slate-colored Junco (*Junco hyemalis*) and the studies of Blanchard on the resident and migratory races of the White-crowned Sparrow (*Zonotrichia leucophrys*). The histologic changes during recrudescence which I have observed in the Oregon Junco are identical in nearly all details to those described and illustrated by Rowan for the Slate-colored Junco.

They agree in part with those described by Blanchard for the Nuttall White-crowned Sparrow. However, the difference in gonadial size between these species is marked.

The histologic changes may be represented by five readily delimited stages which correlate well with the size of the testis.

Stage 1. The size of the testis is at a minimum. In each tubule there is a well-defined row of small spermatogonia ("spermatogonies de premier ordre" of Loisel) close to the basement membrane. The nuclei are usually round, stain darkly, and characteristically show several nucleoli. The outlines of the cell bodies are not well defined in most of the sections, but occasionally the columnar shape of the cells is readily observable. Toward the middle of the tubule and adjacent to the row of spermatogonial nuclei, there are larger, lighter staining nuclei, which are distributed intermittently and show a delicate chromatin network ("spermatogonies de deuxieme ordre" of Loisel). There is no lumen.

The cells between the tubules are closely packed, and may be 4 to 6 cells deep between adjacent tubules. The cells adjoining the basement membrane of the tubule form one or two well-defined rows which completely surround the tubule. The cells in these rows have a small amount of cytoplasm and round or oval shaped nuclei with a well defined, single, centrally located nucleolus. The nuclei are close together and may be elongated in a plane parallel to the surface of the tubule. Some of the cells resemble strongly those of cuboidal epithelium because of the roundness of the nuclei, their regular arrangement, and the lack of any flattening of the cell. Between these rows of cells and in the interstices there are cells which resemble these, but there are also present a small number of cells that are epitheliod in appearance. Rowan calls the cells which invest the tubule, and those in the interstices which resemble them, connective tissue cells. The cells which differ from these are, according to Rowan, "reminiscent of true interstitial tissue but smaller in size" (1939:190). I agree with Rowan that at least two types of cells are present, and rather than say that the small cells are "reminiscent of true interstitial tissue," I regard them as interstitial cells. Their smaller size may be indicative of a lesser amount of activity.

The tunica albuginea is equal in thickness to the short diameter of a tubule, and contains many elongated nuclei.

Judging from Blanchard's descriptions (pp. 53-54) and photographs (pls. 5-6), her Stage 1 (inactive condition) and Stage 2 (first change from inactive condition) are equivalent to the stage just described for juncos. I question whether she could draw a sharp division between testes in Stage 1 and Stage 2. The only distinct characteristic differentiating the two which she gives (p. 53) is that in Stage 2 a "few cells resembling functional interstitial cells . . . are scattered irregularly among the cells of the nonfunctional type [interstitial cells?] which still form six to seven rows between the tubules." Blanchard states that Stage 2 corresponds roughly to "recrudescence" as described by Rowan (1929, p. 190), but a comparison of the two shows that Blanchard's Stage 2 is equivalent to Rowan's description of the winter testis. Rowan's "recrudescence" stage is equivalent to Stage 3 of Blanchard, both of which are definitely distinguishable from the winter testis.

Stage 2. Minor growth changes and variations occur in the winter testis and, as Blanchard found in the Nuttall White-crowned Sparrow, there is a slight increase in volume in the winter (see figure 80).

There has been a marked increase in the number of cells within the tubule. Many of the cells, some of which are primary spermatocytes, are approaching the center of the tubule, and a few

degenerating primary spermatocytes have already reached it. Occasionally mitotic figures are found in large spermatogonia. There still is no lumen.

Because of the increase in the size of the tubules, the connective tissue cells which surround them are extremely elongated and usually only two or three rows separate contiguous tubules. The areas between several adjacent but not contiguous tubules are filled mainly with large epithelioid cells which are interstitial cells. They have large vesicular nuclei with one or two prominent nucleoli. Mixed in with the interstitial cells in small numbers are connective tissue cells. The tunica albuginea is thinner.

This stage corresponds to Stage 3 of Blanchard and is equivalent to Rowan's description of "recrudescence" and to the poorly defined stage which follows "recrudescence."

Stage 3. In this stage the tubules have further increased in size, with the result that most of their surfaces are contiguous. The characteristic cell of this stage is the primary spermatocyte, and in most of the tubules a few of them at least are in that stage of synapsis in which the chromatin lies at one side of the nucleus. A few secondary spermatocytes may be present. Many spermatocytes are degenerating and desquamating cells are freguent in the center of the tubule. A definite lumen is not present, but in some tubules there are small spaces at the center suggesting the beginning of a lumen.

The interstitial cells reach their "maximum" development in the first part of this stage, judging from their numbers and appearance. The cells fill all the triangular spaces available between the tubules, and even occur along the sides of appressed tubules. The connective tissue cells which invest the tubules are extremely flattened and are usually only one or two cell layers deep. Connective tissue cells which resemble those in the previous stages (not investing the tubules), but whose nuclei are larger, are still mixed in with the groups of interstitial cells, but they are not as abundant as the interstitial cells. The tunica albuginea is thinner and more fibrous, with fewer connective tissue cells.

This stage corresponds to Stage 4 of Blanchard and is equivalent to Rowan's "2 mm. diameter" stage. There is complete agreement on the abundance of the interstitial cells at this stage.

Stage 4. From Stage 3 until breeding size is reached, the changes occur with great rapidity. Because of this rapid growth rate, the histologic pictures in testes of different sizes overlap greatly and it is not feasible to characterize accurately more than one stage.

Within the much enlarged tubules with their distinct lumens are secondary spermatocytes, spermatids, and metamorphosing spermatids. At first there is no orientation of the metamorphosing spermatids, but they soon move away from the lumen toward the Sertoli cells and become oriented with their heads toward the basement membrane. As the mature spermatozoa are formed, they are grouped into loosely arranged bundles.

The tubules have enlarged and meet along most of their surfaces. This leaves mainly the triangular spaces, where several tubules fail to meet, for the interstitial cells. The interstitial cells are plentiful, yet reduced in number from Stage 3. Their appearance is identical except for those few which are pressed between contiguous tubules. A few connective tissue cells are present in the interstices with the interstitial cells, and those surrounding the tubules are so flattened that the nuclei almost appear as solid lines. Capillaries are conspicuous and are often filled with corpuscles. In the earlier stages capillaries are rare among the tubules. The tunica albuginea is thin and fibrous.

This stage is equivalent to Rowan's description of testes prior to the attainment of breeding, and comprises Blanchard's Stages 5 and 6. I do not think that Blanchard's Stage 5 is adequately delimited. From her descriptions and photographs, it seems to be more correctly a later phase of Stage 4. It is noteworthy in this connection that on her graphs of the early changes in the testis in both races, Stage 5 is found infrequently when compared with the occurrence of Stage 4, and it occurs practically at the same time as Stage 4.

Stage 5. This is the breeding stage of the testis. The tubules have reached their maximum size and each shows a large, well defined lumen. Mature spermatozoa are closely packed in bundles and their elongated corkscrew-shaped acrosomes are embedded in the Sertoli cells. The bundles of spermatozoa are arranged with extreme regularity along the radii of the tubule. In most of the testes which have been sectioned, free mature spermatozoa were observed and in several where the epididymis has been sectioned, spermatozoa were observed in the lumens of the tubules of the epididymis. Rowan found no free spermatozoa in a male that was mated and engaged in nest building and concluded that "liberation of the sperms apparently does not occur till the time of sexual intercourse."

In recent studies on the motility of spermatozoa in the fowl, Munro (1938) found that the spermatozoa rarely show motility until they have reached the epididymis and show more motility in the vas deferens. It is highly probable that this is true in juncos. Examination of the undiluted fluid of testes at breeding size has shown that numerous mature spermatozoa are present, but that they are not motile. It seems unlikely that Rowan's supposition that the spermatozoa are liberated

from the bundles in the tubules at the time of coitus is correct. It seems rather, that the spermatozoa are freed before coitus and acquire motility and a capacity for fertilization while traversing the duct. More data, however, are needed to establish Munro's observations for juncos. Blanchard has observed mature spermatozoa free in the lumen in the White-crowned Sparrow, and Bissonnette has also demonstrated them in the Starling.

In this stage blood vessels and interstitial cells occur in the small triangular spaces between the tubules. The interstitial cells are similar in appearance to those seen in the earlier stages, but they are reduced in number from Stage 4, and are almost restricted to these triangular areas. Only occasionally are any seen between contiguous surfaces of the tubules. It should be pointed out that although the interstitial cells are reduced in number on each section when compared with sections of testes at Stage 2 and Stage 3, it may be that they are not reduced in number in the whole testis. The volume of the testis in breeding condition may be 100 times the volume of the testis in Stage 2. In addition, there is no reason for supposing that the interstitial cells are any less functional than they are in the earlier stages.

Connective tissue cells which invest the tubules are similar to those in Stage 4, but they are not common in the interstices. The tunica albuginea is extremely thin. The conspicuousness of the blood vessels at this stage is noteworthy.

In the testes of a breeding bird Rowan states (1929:192) that the interstitial cells are "few in number," are "to be found only in some of the triangles between the tubules" and "when they are to be seen they are generally large and easily recognized." This agrees with my observations. Rowan, however, implies that they are scarcer than I have found. Blanchard records the presence of interstitial cells in the triangular spaces between the tubules in testes in breeding condition, but makes no further observations on them.

THE GONADS OF MIGRANT MALES

Gross changes.—The gonads of the migrants were collected from the time that they arrived at Berkeley in October until they migrated at the end of March. In this period the testes only develop to Stage 3, as compared with the attainment of breeding size in the resident race. Through November, December, January, and early February, the testes grow only slightly from their minimum size of 0.5 mm.^{3} to attain an average volume of 1.0 mm.^{3} on February 10. From this date until the end of March, when migration occurs, there is a gradual increase in size with the attainment of an average volume of 4.2 mm.^{3}. These changes are illustrated in the graph (figure 80).

Histologic changes.—The histologic changes and the average volumes for each stage are approximately the same in the residents and migrants. However, there is marked difference in the time of the attainment of the stages and in their duration.

In Stages 2 and 3 the interstitial cells are abundant and just as numerous in the resident race as in the migratory race. When the migrants leave Berkeley, their testes are either in Stage 2 or Stage 3. Blanchard's studies on the interstitial tissue in the resident and migratory races of the White-crowned Sparrow agree with my observations in the Oregon Junco.

The occurrence of abundant interstitial tissue in a resident bird does not invalidate Rowan's conclusion on the role of the interstitial cells in a migrant, but as will be discussed later, other available evidence indicates that the gonads may not be an essential factor in the stimulus for the spring migration. Rowan (1932) has shown that this is true for the fall migration.

COMPARISON OF DATE AND RATE OF ATTAINMENT OF GONADIAL STAGES IN RESIDENTS AND MIGRANTS

The differences in date of attainment and duration of Stages 1, 2, and 3 are well illustrated in figure 80. A brief summary of these differences follows. (1) Stage 1 is of shorter duration in the resident birds; it ends about January 19 whereas in the migrant it does not end until February 21. (2) Stage 2 has an average duration of 15 days, and ends about February 3 in the resident; in the migrant it has an average duration of 28

days, and ends about March 20. (3) Stage 3 in the resident has an average duration of 24 days, and ends about February 27. In the migrant no material is available to indicate when Stage 3 ends. From Rowan's data, Slate-colored Juncos arrive at Edmonton, Alberta, early in April with their gonads in Stage 3. (4) After Stage 3, in the residents, the growth rate is so rapid that full breeding condition is reached by the time the migrants leave. An adequate number of testes of these later stages is not available, and it is not possible to calculate the average duration of Stage 4 or Stage 5. An estimation of the length of Stage 4 is 25 days; Stage 5 appears usually at the end of March.

This marked contrast in development of the gonads under identical external conditions has also been demonstrated in the experiments on induced migration. These observations on the gonads of wild juncos agree with similar observations of Blanchard on the White-crowned Sparrow.

INDIVIDUAL, RACIAL, AND ANNUAL VARIATION IN THE GROWTH OF THE TESTES

Individual.—The residents show more individual variation in the rate of growth of the testes than do the migrants. This is to be expected because of the rapidity of growth of their testes in a short period, and also because their breeding season is longer. The migrants only go through a small part of their testicular growth on the wintering grounds, and due to the small range in volume and the slow growth rate at this time, one does not expect nor observe a large amount of variation. The graphs (figures 80 and 81) show the large amount of variation in volume which is found in the testes of residents collected on any one day. Variation is greatest when the testes are first changing from the winter condition, and after Stage 3 when growth is extremely rapid.

One cause of the variation is possibly the difference in age of the birds. In the samples taken, there probably were birds ranging in age from 1 to 4 years and also immatures. In juncos it is impossible to distinguish the immatures from the adults after December. By that time the skull is usually ossified completely and the plumages are essentially identical. There is no evidence from Blanchard's work, where immatures and adults are separable until March, that any significant and consistent differences occur in the early growth of the testes of immatures and adult White-crowned Sparrows. When it was possible to separate adults and immatures, their testes were usually in the winter condition and no significant differences were found. When subjected to experimental treatment, the immatures and adults show no difference in response.

Racial variation.—Because of the great differences in the distance from Berkeley of the breeding grounds of the several migratory races of juncos, it was thought that it would be worthwhile to determine whether there are differences in testicular growth in these races on the wintering grounds and whether there are differences in the stage of the testis when migration was begun. The pertinent data were analyzed, but show that there are no statistically significant and consistent differences among the races on these points. For this reason a composite growth curve was made which includes all the migratory races (figure 80).

Annual variation.—It was not the purpose of this study on the gonads to analyze the annual differences in the growth of the testis in any of the races. The birds which were available were needed for the experiments. Blanchard, however, studied the annual variation in the attainment of the various stages in the early part of the testis cycle. She concluded that general clemency of weather conditions, especially temperature, for a period of four to nine weeks, depending on the year, beginning December 21 "may allow the cycle to proceed at a rate limited only by the hereditary make-up of the bird; exceptionally unfavorable temperatures can hold back the same hereditary

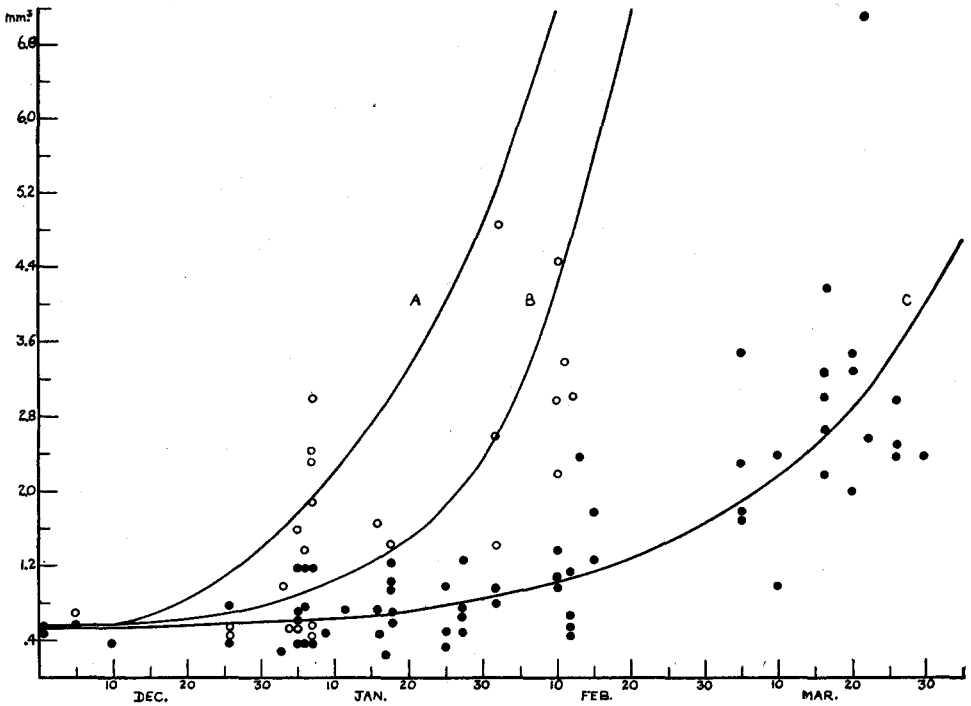

Fig. 80. Volumes of early stages of the testes of resident and migrant Oregon Juncos. A, estimated curve for migrants in induced migration Experiment 2 (no points plotted); B, calculated curve for wild residents; C, calculated curve for wild migrants. Circles=points for curve B; dots=points for curve C.

process . . . " She concludes further (p. 75): "It seems nearest to the truth, then, to think of the gonad cycle as the expression of an inherent annual rhythm . . . which may be modified in part by environmental conditions but it is by no means entirely dependent upon them for its beginning or its general subsequent course." Because of the direct bearing of Blanchard's conclusions on the problem of the annual stimulus for bird migration it is necessary to discuss her data and conclusions.

In comparing the gonadial cycles of different years it is imperative to establish the normal, average gonadial cycle for each year. To do this, one should have a large number of gonads throughout the periods which are being compared and calculate the most probable growth curve. Blanchard did not calculate the average growth rate for each year. Stage 5 (of Blanchard; note comments on identity of Stage 5 on page 253) "is the earliest point in the cycle which is represented by sufficient material to be comparable in all four years (p. 57)." In 1936, two testes were collected at Stage 5; in 1938, four; in 1935, two; in 1937, five. The date of attainment of Stage 5 in these years is determined by choosing that date on which "one or more gonads in Stage 5" is first collected. The date is chosen, therefore, without regard for the individual variation which occurs, and probably does not represent the average for the population. I agree with Blanchard that variations may occur from year to year in the gonadial cycles of birds, but before we are ready to define these variations precisely, we should collect many samples in each year and over a period of years. Then we would be more justified in comparing the growth rates for these years. What the cause of these variations would

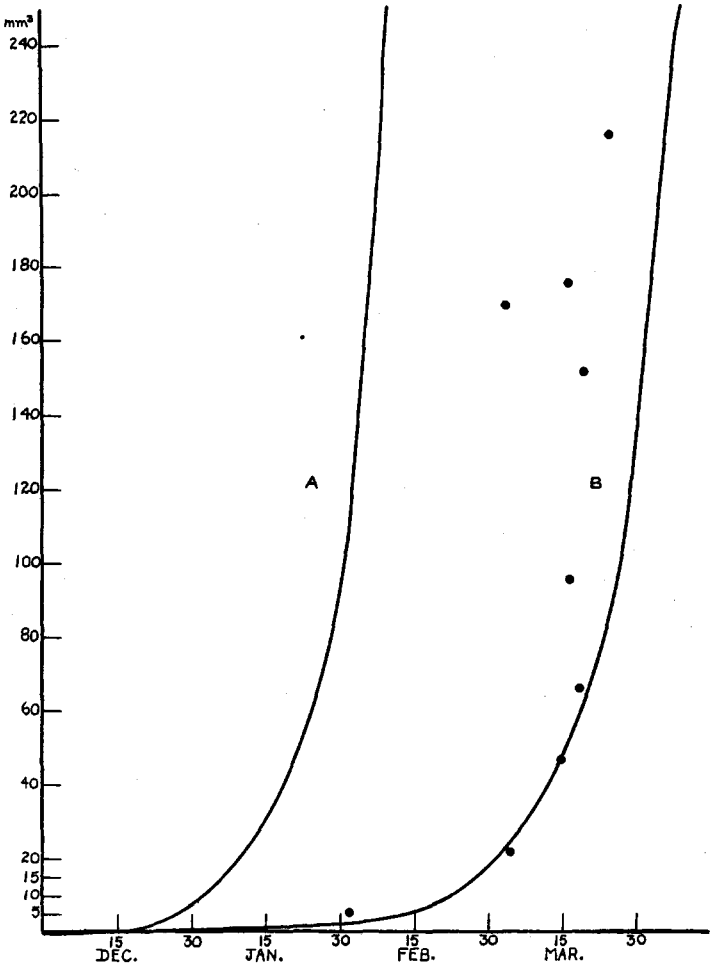

Fig. 81. Volumes of later stages of the testes of resident Oregon Juncos. A, estimated curve in Experiment 2; B, calculated curve for wild birds. Dots=points for curve B; no points plotted for curve A.

be, however, is an extremely complex and difficult problem. The external factors which impinge upon the physiological state of the bird are just beginning to be studied, and concerning the problem of how these factors effect changes in the physiological state of the bird we have only a few theories.

If we accept Blanchard's conclusion (p. 74) that as far as the Nuttall White-crowned Sparrow is concerned, "temperature is the most important single factor lying at the ultimate source of annual variations of the gonad cycle," I cannot see that it follows that it is "extremely doubtful whether the abundant means [experiments involving increases in day length] which have been discovered for upsetting the physiological balance of captive birds should be accepted as possessing any bearing whatever on the factors which control the cycle under natural conditions" (p. 76). Blanchard has presented evidence to show that annual variations in temperature can modify the rate of growth of the testis in a critical period; more data is necessary to prove this conclusively, and I think that it could be proven. However, Blanchard presented no direct evidence for

her view that the length of day should not be accepted as possessing any bearing on the problem of the factors which control the gonadial cycle under natural conditions.

TESTIS SIZE AND FAT DEPOSITION

In the migrant races the growth of the gonads is accompanied by the deposition of subcutaneous and intraperitoneal fat. The classes which are used to denote the fat condition have been described. Although there is considerable individual variation in the fat condition as the gonads develop, it is generally true that the migrants become progressively fatter as the testes grow so that they are usually in the "heavy" class at the time of migration. In the resident race not one individual has been observed which had a heavy deposit of fat. Most of the resident individuals collected in midwinter have a "little" fat; a few only have been taken in the five years of study which have had a "medium" deposit of fat.

THE HISTOLOGY OF THE GONADS OF EXPERIMENTAL BIRDS

Induced migration experiments.—The gonads of the experimentals are similar to those of wild birds in histologic detail and in the volumes of the testes in each stage. The rate of growth of the testes, however, differs markedly. In the experiments, the residents and migrants reach a stage of development which normally takes 100 days in about 50 days. The testes of the residents grew in Experiment 2 from the minimum volume of 0.5 mm.^{3} on December 10 to a volume of 224 mm.^{3} on February 2. The testes of the migrants grew from the same minimum volume to an average volume of 10 mm.^{3} on February 2. The growth rate in each case was a little over twice the normal rate. An equally spectacular difference in the response of the testes of residents and migrants under identical environmental conditions was shown in Experiments 1 and 3 (see tables 1, 3, 8, and 10 and figures 80 and 81).

Delayed migration experiments.—Histological studies of the gonads of birds which were sampled in connection with these experiments confirm the previous conclusion that they were in breeding condition and demonstrate that this condition of the migrant testes is identical histologically with breeding condition in the residents.

THE GONADS OF THE FEMALE

The ovaries which have been collected do not show any readily discernible differences which would aid our understanding of the problem of the role of the gonads in the regulation of migration. If we can solve this problem in the male, where the situation seems to be less complex, we will probably be nearer to the solution of the problem in the female. A few observations, however, have been made which are worthy of mention.

There is a large amount of variation in the size of the largest follicle, which Rowan uses as a criterion for ovarian development, in the ovary in winter. (Rowan's observations were made on only a few ovaries.) As spring approaches, there is a general tendency for the ovaries to show more enlarged ova. When the migrants leave Berkeley and the residents are ready to breed, the condition of the ovary is extremely variable, but on the whole the ova are increased in size over the winter condition. The oviducts show no gross changes. As is well known in other birds, most of the development of the ovary takes place extremely rapidly only a short time before ovulation. The mechanism which brings about this change is not known.

In the induced migration experiments, the ovaries show only a slight response to the increasing day lengths, and there is no gross change in the oviduct. The majority of the females need a longer time than the males for the deposition of fat, and only in Experiment 3 were good results obtained in inducing the females to migrate. These

facts, in contrast to those in the male, suggest that in the female behavior may play a part in regulating the development of the ovary from its condition before breeding until ovulation occurs. In the delayed migration experiments the ovaries show a slight advance in development over their state in March, and the oviducts are slightly enlarged. When compared with the ovaries and oviducts of birds which are laying or incubating in May, however, the advance in development is negligible. A behavioristic stimulus for the late and rapid development of the ovary prior to nesting again suggests itself.

DISCUSSION AND CONCLUSIONS

From the results of the preceding studies it seems that both external and internal factors are involved in inducing the spring migration of the Oregon Junco.

The external factor of prime importance is the length of day, and the regular increases in the day length during the winter and spring effect changes in the physiological state of the bird. These changes are manifested by the growth of the testes, the increase in the secretory activity of the pituitary gland (unpublished data), and the deposition of large amounts of subcutaneous and intraperitoneal fat. Because of these changes, the physiologic state prior to migration is so altered from that which prevailed in midwinter that it provides the internal stimulus which releases the nervous mechanism that controls migratory behavior. It seems, furthermore, that the total physiological state is important and not the physiological condition of one organ alone, such as the gonad. Although the condition of each part makes up the whole, some part, such as the pituitary, may be sufficiently dominant in the physiology of the organism ultimately to determine the total physiological state and hence the type of behavior exhibited.

In the induced migration experiments the juncos undertook a northward migration two months earlier than usual because they were brought into a physiological and psychological state similar to that which prevails at the normal time of migration. When this physiological state was not reached in some individuals, as indicated by the lack of a heavy deposition of fat, they did not migrate. Although increases in day length were employed in the experiments to induce gonadial growth, under natural conditions the period of relatively constant day lengths prior to December 21 may be a factor in the initiation of gonadial development.

If the spring migration is only under the direct control of recrudescing gonads, as Rowan and others maintain, the migrants that were released with their gonads in breeding condition in the experiments on delayed migration should not have migrated. When compared with wild, migratory juncos that had been on their breeding grounds for several weeks, the released migrants had one thing in common with them, namely, gonads of approximately the same condition. They differed from them in several respects: they were not on their normal breeding grounds; they had been forced to flock together in captivity; they had not expended the energy required by migration; and they were heavily laden with fat. Because of these differences, the physiological and psychological state of the migrants that were released was sufficiently similar to that state at the normal time of migration to prevent immediate breeding and to induce migration two months later than usual. When this state was not sufficiently similar to that at the normal time of migration, as indicated by an inadequate amount of stored fat, the juncos failed to migrate. This was demonstrated by 2 out of a total of 87 juncos that were released in the three experiments.

According to the results of Rowan's experiments, juncos that have gonads in breeding condition do not migrate, yet the juncos that were released in our delayed

migration experiments had gonads in breeding condition and they did migrate. A possible explanation of the discrepancy in results has been offered (Wolfson, 1940).

To relate the recent discoveries in endocrinology to migration, Bissonnette (1937) proposed a theory of migration involving the relationship of the gonads and pituitary. He states that there is an inherent rhythm of activity of the pituitary and that the gonads, therefore, are controlled by the cyclic activity of this gland. 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." On recovery of the pituitary the birds are stimulated to migrate before, or while, their gonads recrudesce. Eventually the recrudescence of the gonads reaches such a point as to induce migration to stop and mating to occur. Detention in the winter range, therefore, should be followed by a breeding cycle there. The results of the experiments in delayed migration do not support Bissonnette's contention on the role of the gonads in migration. Although the juncos were detained on their wintering grounds, and their gonads attained breeding condition, they did not breed when they were released, but they migrated.

It seems that the gonads may not be an essential part of the internal stimulus for the spring migration, but rather that the pituitary is the primary controlling factor. I think that the recrudescence of the gonads may be looked upon as a concomitant result of the increase in the secretory activity of the pituitary gland, which probably also results in the increased activity of other endocrine glands, such as the thyroid and adrenals. In relation to migration, the important effect of the changes in the pituitary is not the recrudescence of the gonads, but the production of a physiological state that will enable the bird to meet successfully the energy requirements of migration. If the physiological state is such that a bird could not successfully meet these requirements, migration would not occur because the nervous mechanism which controls migratory behavior would not have been released. Therefore, the most important manifestation of a readiness to migrate is the presence of a large amount of stored fat.

Further evidence suggesting that the gonads may not be an essential part of the physiological state which provides the stimulus for the spring migration is the fact that castrated birds will migrate northward and will return to their wintering grounds in the fall. The results of studies of Dr. John T. Emlen (personal communication) on Gambel White-crowned Sparrows are the basis for this statement. Castration was performed prior to migration, and three birds that were retaken in subsequent winters showed no signs of gonadial tissue. Hann (1941) has shown also that several species of fringillids that were castrated undertook a spring migration.

In addition, the fact that castrated birds will migrate and juncos will migrate with their gonads in breeding condition seems to indicate that migration and breeding are separate entities in the life cycle of a bird, migration being independent of the breeding cycle. One can postulate that in the phylogeny of a species, migration was imposed on an already existing breeding cycle and "timed" to it through the action of the environment and natural selection.

It would seem, therefore, on the basis of the foregoing discussion, that Rowan's theory, which states that the stimulus for the spring migration is the secretion of the interstitial cells in the early stages of recrudescence, is not tenable for the Oregon Junco, and probably not for other birds.

Whether there exists an inherent or genetically fixed rhythm of the endocrine system which is independent of environmental factors for its initiation and subsequent course as maintained by Blanchard (1941) and Woodbury (1941) and suggested in part by Bissonnette is difficult to say. It is known that the maximum activity of the

pituitary and gonads such as occurs in the breeding period cannot be maintained indefinitely; these glands will automatically regress after a period of peak activity. I agree with Bissonnette that this automatic regression is inherent in the endocrine system, and further, that a period of refractoriness during which the pituitary and gonads cannot be stimulated by experimental increases in day length follows this regression. An experiment which was performed to induce gonadial recrudescence in the fall indicates that such a period exists in juncos (unpublished data). In a strict sense this part of the cycle is inherent in that it is due to the inherent qualities of the glands themselves. However, when the endocrine system has recovered to the point where it will respond to changes in day length, I do not think that the subsequent changes in the gonads and pituitary occur automatically and independently of environmental conditions as regression does, but that these changes are under the direct influence of the length of day and modifiable by other factors in the environment such as temperature and food (Kendeigh, 1934, 1941). If this were not true it would be difficult to explain the nearly perfect coincidence of migration, or of nesting, in birds hatched one to three months apart. The inhibitory effect on gonadial growth when birds are subjected to short, constant day lengths, as shown by Rowan (1929, 1937) and Kirschbaum and Ringoen (1936), would tend to support the view that the changes in day length influence the course of development of the gonads. Further, the fact that the pituitary of the Oregon Junco responded to increases in day length in December and January, and migration was induced two months earlier than usual seems to show that the recovery of the pituitary after the refractory period is not genetically fixed, but rather that it is under the control of the environment.

It was demonstrated in the Oregon Junco that gonadial recrudescence as well as the activity of the pituitary (unpublished data) differs in residents and migrants under the natural conditions of winter. The existence of an automatic, inherent rhythm could explain this difference. However, it may also be explained by a difference in threshold of response to the length of day. That this difference in response could be produced two months earlier than usual by artificial increases in day length supports this view. The fact that resident and migratory races of White-crowned Sparrows responded to experimental increases in day length (unpublished data) and showed a similar gonadial response to that obtained in resident and migratory juncos, argues against Blanchard's contention that the difference in the recrudescence of the gonads of these races is due to an automatic, inherent rhythm.

Although a single factor of the environment—length of day (and conversely length of night)—has been stressed in this study as a regulator of the endocrine system in the Oregon Junco, there is no reason to believe that it is the only environmental factor involved in this and other species. That it is a primary factor in many species is generally agreed, but certainly other factors in the environment such as temperature (and weather conditions in general), food, and the presence of other individuals of the species play some part in controlling and modifying the activity of the endocrine system. In some species it is known that one or more of these factors may be the primary controlling factor, and not the length of day (see Marshall, 1942).

Finally, it must be emphasized that no claim is made for the general application of the conclusions which have been presented for the Oregon Junco. The marked difference between resident and migratory individuals of the same species in their gonadial response to light is indicative of the caution which must be exercised in assuming general application of conclusions. It is to be expected that there will be differences among species, and even among members of a species, in their response to environmental conditions and the internal factors which regulate spring migration.

SUMMARY

Resident and migratory races of the Oregon Junco (*Junco oreganus*) were employed in experiments in induced and delayed migration. Three experiments in induced migration involved the release of migrants and residents in late January or February after they had been subjected to artificial increases in day length beginning early in December. Those individuals which responded to the light treatment, as evidenced by recrudescence of gonads and assumption of fat, undertook a northward migration two months earlier than usual. Three experiments in delayed migration involved the retention of migrants at Berkeley until the end of May or early in June, when they were released with their gonads in breeding condition. The results indicate that the juncos undertook a northward migration two months later than usual.

Studies of the gonads have shown that residents (*Junco oreganus pinosus*) and migrants (*J. o. thurberi, J. o. shufeldti, J. o. montanus,* and *J. o. oreganus*) differ in their gonadial cycles, although they flock together in the winter and are subjected to the same environmental conditions. The testes of the residents recrudesce earlier and at a faster rate than those of the migrants. When the migrants leave Berkeley at the end of March, their testes have an average volume of 4 mm.^{3} whereas the testes of the residents have an average volume of 220 mm.^{3} This difference in growth rate has also been demonstrated under experimental conditions. Histologically the testes of residents and migrants are identical. Interstitial cells occur in the testis at all stages from the winter condition to the breeding condition. They appear to be more abundant in the early stages of recrudescence, but this may be due to the small volume of the whole testis in these early stages. Individual variation in size of testis is marked in the residents during the period of rapid growth prior to breeding. No significant variation in testis growth and size at time of departure is found among the migratory races.

Histological studies of the gonads of experimental birds revealed that the gonads were at breeding condition at the time of release in the delayed migration experiments and that in the induced migration experiments the testes were histologically identical to those at the normal time of migration.

In the migrants there is a heavy deposition of subcutaneous and intraperitoneal fat at the time of migration. The residents show no such deposition of fat.

The ovary shows little change from winter to spring compared with its development immediately before laying. In the experiments the ovarian response was negligible.

On the strength of our present knowledge of the relation of the hypothalamus to sleep and the gonadotropic activity of the pituitary, the following explanation of how increases in day length can cause recrudescence of the gonads under experimental and natural conditions is advocated. As the days increase in length, birds are awake for longer periods of time because the state of wakefulness, at least in some birds, is a conditioned response to light; the concomitant activity of the hypothalamus causes an increased production, or release, or both, of the gonadotropic hormones of the pituitary; these in turn stimulate gonadial recrudescence.

It is concluded that internal and external factors regulate the spring migration of the Oregon Junco. The external factor of prime importance in juncos is the length of day. As the days increase in length in the winter, the birds are awake for longer periods. Associated with these longer periods of wakefulness is an increase in the duration of activity of the hypothalamus (Wolfson, 1941). This causes an increase in the production, or release, or both, of gonadotropic and other hormones from the pituitary. These hormones produce physiological changes in the bird, as exemplified by the

recrudescence of the gonads and the deposition of large amounts of fat. Because of these changes, the physiological state prior to migration is so altered from that which prevails in midwinter that it provides the internal stimulus for the spring migration. The internal stimulus induces the actual migration by releasing the nervous mechanism which controls migratory behavior.

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