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A PRELIMINARY REPORT ON SOME EXPERIMENTS ON BIRD MIGRATION

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When Rowan (Proc. Boston Soc. Nat. Hist., vol. 39, 1929, pp. 151-208) discovered that it was possible to cause recrudescence of the gonads of birds after the breeding season by artificially lengthening the periods of daylight, he performed several experiments on bird migration which involved the releasing of birds with their gonads at various stages of development. From his results Rowan concluded that birds released with their gonads at winter minimum or spring maximum showed no inclination to migrate, whereas those released with their gonads either in a state of recrudescence or regression departed upon gaining their freedom. From histological studies, he concluded that interstitial tissue occurs abundantly in gonads that are regressing or recrudescing, but is "wanting in the resting state of the winter testis and if present at all in the summer is but sparsely represented" (*op. cit.*, p. 203). These conclusions are the basis for Rowan's theory of the mechanism of annual migration. This theory states that the secretion of the interstitial cells of the gonads is responsible for arousing migratory behavior, and that with the disappearance of this tissue the stimulus to migrate lapses. From the results of later work with crows (Proc. Nat. Acad. Sci., vol. 18, 1932, pp. 639-654), however, Rowan concluded that the southward passage "appears to be independent of the influence of the gonads."

The problem of how the increasing day length induces gonadial development has received the most emphasis since Rowan's initial work, but little or no experimentation has been done on migration *per se*.

To relate the recent discoveries in endocrinology to migration, Bissonnette (Wilson Bull., vol. 49, 1937, pp. 262-264) has proposed a theory involving the relationship of the gonads and pituitary. He believes 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 sex glands 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.

According to Rowan and Bissonnette, migratory birds which are retained on their wintering grounds and released when their gonads attain breeding condition should *not* migrate. The purpose of this report is to describe two experiments undertaken to test this hypothesis.

Method.—The species used 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 two reasons. First, the birds of this species could be obtained in adequate numbers and kept in captivity. Second, and most important, the species contains both migratory and resident races. The migratory races used were *J. o. oreganus*, *J. o. shu-*

feldti, J. o. thurberi, and *J. o. montanus.* The most northern race is *oreganus* which breeds as far north as Yakutat Bay, Alaska. South of this race, *shufeldti* and *montanus* breed, the former in the central coastal areas and the latter in the far interior. *Thurberi* is the most southern, breeding in the coastal regions of northern California and in the Transition and Boreal zones in the mountains that extend south to San Diego County. All of these races winter south of their breeding grounds except some populations of *thurberi* which winter merely at lower altitudes. The breeding range of the resident race, *J. o. pinosus,* extends from San Francisco Bay south to San Luis Obispo County. Berkeley, therefore, is at the northern limit of its range.

The first experiment was completed in June, 1938, the second in June, 1939.

The birds were trapped in Potter traps at the poultry laboratory in Strawberry Canyon on the campus of the University of California, Berkeley, from the beginning of December, each year, until the last week in March, when the migrants usually leave. All races were found about equally abundant in the flocks, with the exception of *montanus* which was infrequent. The birds were identified to race by comparing them with specimens at the Museum of Vertebrate Zoology. Any individual which could not be identified beyond doubt as a migrant or a resident was released. Those retained were housed in 8′x 8′x 8′ outdoor cages situated in a live oak-California bay habitat in Strawberry Canyon. Their food consisted of canary seed.

Not knowing whether the gonads of migrants would develop to full breeding size at the latitude of Berkeley, the birds in experiment 1 were divided into two groups, the experimentals which received additional light after sunset, and the controls which received no artificial light. Lighting was begun on April 2 and continued until May 23, the day of release, when normal, wild migratory individuals were nesting and probably incubating on their breeding grounds to the north. Samples were taken of the migratory experimental and control birds on April 29 to test the efficacy of the additional light, and also on May 23 and 24. At the time of release all birds were banded with U. S. B. S. numbered bands. In addition, small curved chicken feathers were dyed various colors and attached to the bases of the tails with Duco cement. With the aid of these colored feathers, the behavior of the resident and migratory races after release could be recorded. No attempt was made to retrap or collect any of the migrants until they had been free for at least twenty-four hours, thereby allowing sufficient time for readjustment. After that period any migrant seen was collected and sampled to determine the condition of the gonads, fat storage, and general health. The gonads and the pituitary glands were saved for microscopic study.

The method in experiment 2 differed only in that the birds received no additional lighting and were released on June 5. In experiment 1, it was found that the controls which received no artificial lighting reached almost the same gonadial size as the experimentals. Therefore, the release was made two weeks later than in the previous year to insure as complete a development of the gonads as possible.

Most of the gonads and pituitaries that were sampled were fixed in Bouin's fluid, a few in Zenker-formol. The 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. Since none of the fixed material has been sectioned yet, only the testis sizes can be given to indicate the degree of development. That the size of the testis is a reliable indication of internal structure has been shown by Rowan, Bissonnette, and others who have worked on male gonadial cycles. The ovaries cannot be described definitely until studied microscopically and many data, therefore, cannot be given at this time.

The fat condition of each sample, an important fact which was not mentioned by Rowan, is estimated. It is recorded in four classes: no fat, little fat, medium fat, and heavy fat. Occasionally plus and minus are used to indicate extremes. These classes include not only the amount of fat, but also its distribution. In a bird with "little fat," there will almost always be some between the branches of the furculum and along the pterylæ, but practically none in the abdominal region, on the flanks, and on the lower part of the back. In the "medium" class, the fat is more abundant about the furculum and pterylæ and it begins to be visible in nearly all of the aforementioned locations. In the "heavy" class, the fat is further increased in amount in all these regions, especially in the abdomen and lower back where a layer 1/8 of an inch thick may be found.

Releases.—Experiment 1. The number of birds released on May 23 was 39, 34 (17♂♂, 14♀♀, 3?) migrants and 5 (2♂♂, 3♀♀) residents. The numbers of each migratory race will not be given at the present time because there are insufficient data to indicate significant differences between those races that winter at different distances from their breeding grounds. When more data have been obtained, these numbers will be presented. It is significant that two of the experimental birds had been banded previously in Strawberry Canyon. These were: C41885, ♂ *montanus* (hybrid with *J. hyemalis*), banded March 8, 1932, and 36-15127, ♀ *pinosus*, banded December 12, 1935.

Experiment 2. Thirty-two birds were released on June 5, 27 migrants (15♂♂, 12♀♀) and 5 (♂♂) residents. Of the 32, 6 had been banded previously and had repeated several times before they were used in the experiment. They were, therefore, familiar with the immediate vicinity and demonstrated a "homing instinct."

Samples.—The condition of the twelve samples taken in experiment 1 and the six in experiment 2 are given in table 1. In the first samples only the length of the left testis was measured. Fluid was extracted from all testes that were over six millimeters long to determine the presence of mature, free spermatozoa. Sperms were readily observed in all cases, but showed no motility.

TABLE 1. SAMPLES TAKEN IN EXPERIMENTS 1 AND 2

Date	Identification	Weight	Gonads	Fat
		Experiment 1—1938		
April 29	Exp. ♂ shufeldti	16.1 g.	L, 6.2 mm. (length)	Medium
	Exp. ♂ oreganus	18.9	L, 7.3 (length)	Heavy
	Cont. ♂ thurberi	18.0	L, 3.4 (length)	Heavy
	Cont. ♀ oreganus	18.2	Follicles enlarged	Heavy
May 23	Exp. ♂ pinosus	19.0	L, 8.5 x 6.4 R, 7.0 x 6.6	None
	Exp. ♀ oreganus	18.0	Largest follicle—1.7	Heavy
	Cont. ♂ oreganus	21.1	L, 6.1 x 4.2 R, 5.1 x 4.6	Heavy+
	Cont. ♀ shufeldti	21.8	Follicles enlarged	Heavy+
May 24	Exp. ♂ shufeldti	19.4	L, 8.4 x 6.2 R, 6.5 x 6.5	Medium+
	Exp. ♀ shufeldti	15.3	Largest follicle—1.0	Little
	Cont. ♂ shufeldti	16.4	L, 7.9 x 5.3 R, 6.9 x 5.9	Medium
	Cont. ♀ pinosus	15.4	Largest follicle—1.2	None
		Experiment 2—1939		
April 28	♂ shufeldti	18.5	L, 6.1 x 4.8 R, 5.4 x 4.7	Heavy
April 29	♂ thurberi	19.9	L, 3.6 x 3.1 R, 2.9 x 3.1	Heavy+
	♀ shufeldti	19.0	Follicles much enlarged	Heavy

June 7	♂ shufeldti	17.6	L, 7.6 x 6.1 R, 6.8 x 6.3	Heavy
	♂ shufeldti	15.4	L, 7.1 x 5.6 R, 6.9 x 6.7	Little—
	♀ shufeldti	18.1	Largest follicle—1.5	Heavy

Judging from the data obtained from the samples, the gonads of the birds that were released must have been in breeding condition. This is certain in the males where testis size and presence of spermatozoa are diagnostic. In the females the ovaries contained enlarged follicles which were about as large as follicles in wild birds that have mated and begun to nest.

Behavior at the time of releasing and retrapping.—The behavior on the day of release differed in the two experiments. In experiment 1, the birds were released at 8:00 a. m., May 23, 1938, by opening the doors of the cages. Food and water were available inside and outside of the cages. Within forty minutes most of the birds were free. A summary of the prevailing behavior follows.

There was no flocking as is observed in wintering birds, but on the contrary there was much singing, fighting, and chasing among the experimentals as well as the controls, among the residents as well as the migrants. This type of behavior was not seen in the cages prior to release. Was this normal behavior connected with territorial establishment, or was it a "natural" reaction to the newly gained freedom? Occasionally the birds flew into the cages to feed or bathe. The behavior was similar throughout the day, but the amount of activity diminished as the birds spread out. At 6:00 p. m. of the same day about twenty-five birds were seen feeding in and around the cages. Singing, fighting, and chasing were not observed, and no winter flocking behavior was exhibited. The birds behaved as individuals. On May 24, I returned to the cages at 8:00 a. m. and saw only one pair (♂, ♀) of *pinosus* on the cages and heard one bird singing in the tree above. This also was a *pinosus*. Upon searching the area near the cages, one control migrant was seen foraging with a *pinosus*. Leaving the area near the cages, other parts of Strawberry Canyon were searched, but no other marked bird was found. Later that day, the same pair of *pinosus* (male identified by colored band) was again seen on the cages, but the control migrant could not be found, nor the other *pinosus*.

During the following days, until June 7, when I left Berkeley, the canyon was searched and traps were set, but no additional marked birds were seen. The pair of *pinosus* could be found any day during that period near the cages.

At the end of July, I resumed trapping and observing in the canyon, but only one experimental resident was found on July 21, 1938. This was 36-15127, ♀ *pinosus*, originally banded on December 12, 1935. This bird was probably a member of the pair observed earlier.

Of the 34 migratory birds released, 8 were retrapped at the poultry ranch after the breeding season, 3 in the winter of 1938, 1 in the spring of 1939, 3 in the fall of 1939, and 1 in January, 1940. Of the five resident birds released 4 are accounted for, 2 females which were retrapped, and 2 males which were seen after the release.

In experiment 2 the birds were released from Potter traps, in which they had been all night, at 10:00 a. m. on June 5, 1939. As they were released, they flew directly into the trees over the cages and in an extremely short time there was no evidence of their presence. There was no singing, fighting or chasing. Flocking behavior was not observed. In the course of the day the birds did not come to the ground to feed, and they could not be found in the dense foliage. On June 6, upon returning to the cages at 8:00 a. m., two *pinosus* and one migrant were seen. They were observed several times during the morning. In the afternoon, twenty-seven hours after the release, the migrant, 39-61008,

♂ *shufeldti*, was collected and sampled. The testes measured as follows: left, 7.2 x 5.3, right, 7.0 x 5.3. This is approximately similar to those of breeding birds. However, the bird had little stored fat in contrast to two of the three samples taken on June 7, which showed heavy fat. The *pinosus* were not collected and the canyon was not searched again, for I left Berkeley on June 7. After returning on June 19 many trips were made into Strawberry Canyon until early August, when trapping was begun. One marked *pinosus* was seen, but not collected. At the time of writing, January, 1940, two migrants have been retrapped, in November and December, 1939.

Conclusions.—From the results of these experiments, it seems probable that birds with their gonads in a state different from that at which they normally migrate will migrate in the spring as late as sixty days after their normal date of departure. In the males that were released the testes were at breeding size, 7-8 mm. long, whereas the males normally begin to migrate when their testes are 1.8 to 2.5 mm. long. In the females the development of the ovary was definitely more advanced than the state of the ovary at the time of normal migration. It was probably similar to the ovary of birds at the beginning of nesting, but not until microscopic studies have been completed can exact measurements of follicles be given.

The problem of whether the birds undertook a migration or were only a few miles away was approached by trapping studies. Many wild residents and migrants were banded in two successive years in the period from November through February. All races were retrapped frequently at the poultry laboratory during the winter period up until the time of northward migration in late March. After that time only residents were retrapped and migrants did not repeat until southward migration had occurred in late fall. We conclude, therefore, that migrant and resident races exhibit a well developed "homing instinct," that individuals of migrant races which winter in the canyon can be found there more or less continually until they migrate northward, and that those of the resident race are sedentary. After our releases, the experimental residents were retrapped or seen, but the migrants were not retrapped until subsequent southward migrations had occurred and wild migrants returned to the canyon. The similarity between these trapping records of wild and experimental birds can best be explained by the assumption that the experimental migrants undertook a northward migration.

Discussion.—According to Rowan's theory of the mechanism of annual migration, juncos with their gonads in breeding condition should not depart. How then can our results be explained? Rowan based his theory on juncos brought into maximum gonadial condition in December, and released at that time. Our birds were released with their gonads in breeding condition in May and June. This circumstance may offer an explanation. However, I believe that it is more probable that the discrepancy in results comes from differences in method other than the factor of time of year when releases were made. The following criticisms may be offered to support this belief.

1. Rowan states that his experimental birds were in good condition when released, but he does not describe the fat condition of the birds, so important in indicating a readiness to migrate.

2. Rowan allowed only about three hours (9:00 a. m. to 12:00 m.) to elapse before retrapping birds which remained. Is this sufficient time to allow for readjustment, particularly when food is scarce naturally and abundant at the traps, and when the birds are in great need of food because of the weather conditions? Examination of his record of banded releases reveals that out of 178 releases, 137 were retrapped. Of these, 86 (about 63 per cent) were retrapped on the day of release and many on the following day. In our first experiment all the birds could have been collected within three hours after the release.

3. Each of Rowan's releases involved few individuals and not all the birds that were retrapped were sampled. This is evident from his table of releases (1929, pp. 178-182) which shows that retrapped birds were used for subsequent releases. Would it not have been better to sample all birds which remained to determine accurately what the condition of the gonads was in each bird, particularly since the number released was small?

4. Rowan concludes (1929, p. 203) that "those [liberated experimentals] that have attained the maximum [testis size] . . . show no inclination to go." Yet, he does not state the number of birds that were released in this condition.

From his description, the only experiment during which the birds may have been released with their gonads at maximum was the experiment of 1926. This experiment, during which the gonad response was irregular, began on October 1 and experimental releases were made in favorable weather on November 15 and 16, and on December 19 and 29, a total of 36 birds being released. Of these, 16 were retrapped. "All male returns were killed for examination and they either had testes still at minimum *or else large and in the early stages of spermatogenesis*" (p. 185; italics mine). According to Rowan's description of the histology, early stages of spermatogenesis are found in testes from 3.0 mm. in diameter upward (mean diameter taken from cross section). How many birds, therefore, were released with their gonads *at maximum,* and has enough evidence been presented to demonstrate that birds with their gonads at this stage showed no inclination to go?

5. Rowan states that the race he used, *Junco hyemalis connectens,* breeds commonly in the latitude of Edmonton, Alberta, where his experiments were conducted, as well as to the north. How then could Rowan distinguish birds which bred in that vicinity from those that migrated in from the north? Assuming that some of his birds had bred at Edmonton, could the experimentals that were released be expected to migrate northward if they had a "homing instinct" and were already on their breeding grounds?

Rowan's experiments proved beyond a doubt that a bird's gonads can be activated or depressed irrespective of temperature by artificially controlling the day length. His theory of migration, however, I do not believe is well founded because of the criticisms given above.

Bissonnette postulated that detention in the winter range should be followed by a breeding cycle there. From the results of my experiments this part of Bissonette's theory does not seem correct.

In conclusion I shall discuss several points which arise from the results of the experiments on *Junco oreganus.* If migratory behavior is under direct control of the gonadial secretions only, as Rowan and others believe, and if breeding behavior is only a function of gonadial condition, then the migrants released should have remained sedentary. Groebbels (Der Vogel, 1932, pp. 757-838) and Kendeigh (Ecol. Monogr., vol. 4, pp. 397-406) have each proposed that there is a general physiological stimulus for initiating migratory behavior. From my results it seems that the total physiological and psychological state of the bird is important in inducing its migratory and breeding behavior and not the physiological condition of one organ alone, such as the gonad. The state of each part makes up the whole, even though some part, such as the pituitary, may be sufficiently dominant in the physiology of the organism ultimately to determine the whole, and hence the type of behavior exhibited.

Compared with wild migratory birds which had been on their normal breeding grounds for a few weeks, the migrants that were released had one thing in common, namely, gonads of approximately the same condition. They differed from wild migrants

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.

The behavior of the released migrants may, therefore be explained by the fact that their physiological and psychological state was sufficiently similar to that state at the normal time of migration to induce migration two months later than usual. This state I believe enables the bird to migrate by releasing the nervous mechanism which controls migratory behavior and by bringing the birds into such a physiological condition that they may successfully meet the energy requirements of migration.

The failure to migrate of the bird caught on June 5, 1939, may be explained by the fact that it lacked a physiological state sufficiently similar to that of normal birds to induce migratory behavior. The dissimilarity may be reflected by the slight amount of fat which this bird had.

According to the above reasoning, resident and migratory races should differ in their physiological states. The few data on this subject that I have collected for *Junco* agree with Blanchard's data (in press) for the resident and migrant races of the White-crowned Sparrow (*Zonotrichia leucophrys*). In the resident race the testes recrudesce earlier and at a faster rate than in the migratory races. In table 2, allowing even for individual variation, the differences may be seen to be great and significant. None of

TABLE 2. TESTIS SIZES OF WILD RESIDENT AND MIGRANT OREGON JUNCOS

Date	Resident	Migrant
February 11, 1939	Left, 1.9 x 1.3 mm.	Left, 1.0 x 0.8 mm.
	Right, 1.7 x 1.4	Right, 0.8 x 0.8
February 12, 1939	Left, 1.8 x 1.3	Left, 1.0 x 0.7
	Right, 1.7 x 1.3	Right, 1.0 x 0.7
March 16, 1939	Left, 4.4 x 3.2	Left, 1.5 x 1.2 (heavy fat)
	Right, 4.0 x 3.3	Right, 1.5 x 1.4
March 20, 1939	(1) Left, 6.0 x 4.9	(1) Left. 1.8 x 1.4 (heavy fat)
	Right, 5.7 x 5.2	Right, 1.6 x 1.3
	(2) Left, 4.8 x 3.4	(2) Left. 1.6 x 1.2 (little fat)
	Right, 4.4 x 3.9	Right, 1.2 x 1.1
March 25, 1939	Left, 7.1 x 5.3	Left, 1.8 x 1.2 (heavy fat)
	Right, 6.3 x 5.8	Right, 1.8 x 1.3

the residents collected has shown a medium or heavy fat condition, and if any fat is present it is of small amount. The resident and migratory birds flock together during the winter and are naturally subjected to the same environmental conditions, yet the cycle of the testes and of fat deposition differ. The response of the internal organs which control the gonads and fat deposition to the same environmental conditions must therefore be different. This difference in response has been shown experimentally also. Resident and migratory juncos were subjected to artificially increased daylengths in December and January. At the close of the experiment the migratory birds showed heavy fat, and their testes averaged 1.5 mm. in length. The resident birds had testes 8.1 mm. long and no fat. A difference in threshold of response is necessary to explain these differing gonadial cycles.

Further studies on the physiology of resident and migrant races show promise of yielding significant data, and these data should lead the way to a better understanding of the annual mechanism of migration in the juncos, and perhaps in other birds.

I wish to express my deep appreciation to Dr. Alden H. Miller whose counsel and advice have been invaluable in the execution of this work and the preparation of this report.

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