THE RELATION OF LIGHT PERIODICITY TO THE REPRODUCTIVE CYCLE, MIGRATION AND DISTRIBUTION OF THE MOURNING DOVE (*ZENAIDURA MACROURA CAROLINENSIS*).[1]

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THE PROBLEM.

THE more obvious relations between the annual migrations of birds and certain facts connected with their reproductive cycle are matters of common knowledge. In the northern hemisphere the summer phase of the migratory oscillation is devoted primarily to reproduction—nest building, incubation and rearing of the young. The winter phase, spent in the lower latitudes, is a period of reproductive inactivity. This applies not alone to behavior, for the reproductive organs themselves, and particularly the gonads, are during this period greatly reduced in size and quiescent in function. Modern researches have shown the functioning of the reproductive system and the resulting secondary effects and behavior to depend upon a series of complex endocrine relations, many of the details of which remain, however, to be worked out. What light can this knowledge throw on migration?

Writers on the problems have advanced many theories to account both for the historical inception of migration and for the semiannual stimulus which initiates the northward movement in the spring and the return movement in the fall. While it has not always been done, this question should be kept quite distinct from what is probably the more difficult riddle, namely, how the birds find their way with such relative accuracy from one region to another and back again. There is no need to review all the explanations that have been offered for even the first of these problems. They will be found detailed in the recent works of Thomson (1926) and Wetmore (1930).

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It has seemed reasonable that there should be some causal connection between the annual migration and the reproductive cycle but there has been disagreement as to which was cause and which effect. Does the change in the reproductive glands and resulting endocrines provide the stimulus for changed behavior, resulting in the migratory movement; or is migration initiated by some extrinsic cause, and are the resulting structural and endocrinal changes secondary? If the former is the case, what is the stimulus that causes the seasonal enlargement of the gonads in the spring and their atrophy in the fall? And if migration is the primary cause, what are the factors that impel the birds to undertake their semiannual journeys?

The recent illuminating experiments and suggestions of Rowan (summarized in his book, 'The Riddle of Migration,' 1931) have afforded a new approach to this age-old problem. Briefly stated, his results, though not yet very extensive, indicate very strongly that migration is a direct sequence of the gonadal changes and the consequent internal endocrine reactions—birds with enlarging gonads and increasing sexual activity have a tendency to move northward, while those in which the gonads are becoming smaller and the sexual activity is decreasing tend to a southward migration. As a corollary, when the gonads remain *in statu quo* the birds "stay put" in whatever region they happen to be. These propositions need to be put to further test, and doubtless modifications will be necessary in special circumstances, but at any rate they furnish an excellent working hypothesis which seems to fit well not only with the experimental results but also with numerous known facts about the migratory movements of birds.

This throws the problem back to the factors which initiate the pre-seasonal and post-seasonal changes in the gonads, and after showing the inadequacy of other causes, such as changing temperature and food supply, Rowan relates these changes to light periodicity, in other words, to the gradual lengthening of the daylight period in the spring and the corresponding shortening of the days in the fall. His experiments furnish convincing proof of this relationship in the birds he worked with (principally Juncoes) and his results have been confirmed in this respect by Bissonnette (1931) for the European Starling. From further experiments

Rowan concluded it was the period of activity of the birds as determined by the daily light duration which was the effective cause of the gonad changes rather than the direct action of the light itself. Bissonnette's findings are somewhat contradictory on this point and he is inclined to believe the result due rather to the direct effect of light rays of particular wave lengths. The need of more experimentation is indicated. As before suggested, it is possible that different species react in different ways. The Junco is preëminently a migratory bird while the Starling is essentially non-migratory.

The Reproductive Cycle.

Our interest in this particular problem began from another angle, before the results of Rowan were announced. For some years we have in this laboratory been making an intensive study of hybridization of various species of pigeons and doves and this has meant breeding a good many of the wild species in confinement. The facts which particularly aroused our interest were in connection with the breeding of captive Mourning Doves (*Zenaidura macroura*), and in particular of one female, No. D169.2, which has a long breeding history.

Our birds are kept in a room in which the heat throughout the winter months is maintained as nearly as possible at 70° F. or a little above. While there are lights in the room, the artificial light is seldom used to extend the daylight period, so that the light periodicity is essentially that normal to the season. All birds receive the same feed, which consists of a grain mixture supplemented with cod-liver oil and occasionally with cottage cheese. In this respect it is uniform throughout the year, except that succulent green feed is occasionally added, such as finely chopped carrots, apples, cabbage or lettuce during the winter months and clover or other green leaves in the summer. In this there is some seasonal variation, but it is important to have in mind that all the birds are treated alike. The same applies to all the other operations related to management.

It was early noticed that while the domesticated Ring Doves (*Streptopelia risoria*) were laying more or less regularly all through the year—with a low period at the time of molting in the fall—

the wild species, on the other hand, showed a much more definite seasonal cycle. This was particularly noticeable of the Mourning Doves and this report will be confined largely to them. The history of female D169.2, referred to above, is particularly interesting. This female was purchased in December 1926 from a game farm in Ohio. Her age and early history are accordingly unknown. She has at various times been mated to two different Mourning Dove males and to a Ring Dove, but so far as can be observed the species of her partner has not affected her reproductive cycle, once the pair is well mated. Her history of production with respect to the beginning and cessation of laying each season follows:[2]

TABLE I.

PRODUCTION HISTORY OF FEMALE MOURNING DOVE, D169.2.

Season	*Date of beginning of laying*	*Date of cessation of laying*	*Length of laying season*
1927.........	May 8	July 25	78 days
1928.........	Mar. 11	Aug. 2	144 "
1929.........	Apr. 19	Aug. 6	109 "
1930.........	Apr. 26	Aug. 16	112 "
1931.........	Apr. 13	Aug. 25	134 "
Average......	Apr. 15	Aug. 9	115 days
Average for 1928–1931..	Apr. 3	Aug. 12	125 days

Taking all five years, it will be seen that while there is considerable variability, this female adhered to a reproductive schedule, in so far as the seasonal cycle is concerned, not greatly different from that of the wild Mourning Doves in this locality, and this in spite of the fact that she did not make a southern migration in the winter, but was in an environment in most respects similar to that of the rest of the year.

The average date at which this female began to lay in the spring is April 15 and the average date of last egg laid in the fall is August 9. It is doubtful whether the first season is strictly comparable to the other since the pair was late in getting started and the male

[2] A study of the egg production and rhythm of the cycle is to be reported separately.

died on August 2. Another male was put with her on August 4 but they failed to mate up that season. It is quite possible that if her former mate had not died she would have extended her laying season. If this season is omitted, the average dates for beginning and cessation of laying are April 3 and August 12, respectively. The difference of these few days is, however, of little consequence in the present connection.

According to Schorger (1929), in Dane County, in which Madison is located, wild Mourning Dove nests with eggs have been found as early as April 18 and as late as September 12. Since nests in the wild may not be found as soon as the eggs are laid, the date of first laying is presumably somewhat earlier than April 18. Similarly, since there is an incubation period of 14 days, eggs might be found for two weeks after they were laid, so the date of last laying may be assumed to be somewhat earlier than September 12. Furthermore, these represent earliest and latest records, respectively, rather than averages, and apply to all observations made and not to a single pair. It may be a fair statement, and sufficiently accurate, to say that in the vicinity of Madison the normal laying period (as distinguished from nesting period) extends from the early or middle part of April to the latter part of August. The time of last laying is undoubtedly largely influenced by the fortuities associated with the late summer brood. If a pair of doves were busy up to the latter part of August with a brood reared from eggs laid early in the month, it is quite likely they would not nest again; but if the earlier nest were broken up or the young died by the middle of the month another nesting would be quite likely.

Similar but less extensive records have been obtained from a few other captive Mourning Dove females. Thus D261J_2 and D261A_3 were mated up in the early summer of 1931. They laid several sets of eggs during the summer, but both stopped laying about August first (D261J_2 last eggs July 27 and 29; D261A_3 last eggs July 31 and August 2).

Evidence that the male goes through a cycle similar to that of the female is indicated by the history of Mourning Dove D261E_2. This bird was hatched in August 1929 and in the following May was mated to a female white Ring Dove. The history of the eggs produced by this pair during the two following seasons is interesting and significant (Table II).

TABLE II.

BREEDING HISTORY OF MALE MOURNING DOVE, D261E_2, MATED TO WHITE RING DOVE, D356.5.

Placed together in mating cage May 29, 1930; transferred to regular cage, May 31.

Eggs	*Date Laid*	*Fertility Record*
A, B	18, 19 June, 1930	Both infertile
C, D	14, 15 July, 1930	Both fertile
E, F	6, 7 Aug., 1930	Both fertile
G, H	3, 4 Sept., 1930	Both infertile
J, K	4, 5 Oct., 1930	Both infertile
L, M	24, 25 Oct., 1930	Both infertile
N	29 Nov., 1930	Infertile
Q, R	28, 29 Dec., 1930	Both infertile
S, T	24, 25 Jan., 1931	Both infertile
U	22 Feb., 1931	Fertile
W, X	16, 17 Mar., 1931	Both fertile
Y, Z	8, 9 Apr., 1931	Both infertile
A_2, B_2	30 Apr., 1 May, 1931	A_2 fertile, B_2 infertile
C_2, D_2	21, 22 May, 1931	Both fertile
E_2, F_2	12, 13 June, 1931	Both fertile
G_2, H_2	4, 5 July, 1931	Both fertile
J_2, K_2	27, 29 July, 1931	Both infertile
L_2, M_2	19, 21 Aug., 1931	Both infertile
N_2	10 Sept., 1931	Infertile
Q_2, R_2	5, 6 Oct., 1931	Both infertile
S_2, T_2	31 Oct., 1 Nov., 1931	Both infertile
V_2	26 Nov., 1931	Infertile

The first thing to be noted in this table is the difference between the laying history of this Ring Dove female and that of the Mourning Dove previously described. Whereas the Mourning Dove began laying in early April and ceased in early August, producing no eggs in the winter months, the Ring Dove laid more or less regularly throughout the entire year. The irregularity is due in part to the varying lengths of time that the eggs were left in the nest.

Fertility, on the other hand, is definitely seasonal. In 1930 the first eggs produced, three weeks after the pair was put together, were infertile, but the eggs produced in July and August developed embryos. After this there was no fertility all through the winter months, but a fertile egg was produced on February 22nd, following which all but three eggs were fertile until the last of July, when fertility definitely ceased.

No extensive study has been made of the change in size of the gonads in relation to season, because of the limited number of birds at our disposal. Such incidental records as have been made, however, on birds that died or were laparotomized, show, as would be expected, that both the ovaries and testes decrease greatly in size and become inactive in the winter months, enlarging again in the spring, as is characteristic of most birds. Both Rowan and Bissonnette have shown that similar changes in size and activity are caused by the changed light periodicity.

Relation to Light Periodicity.

While based on relatively few birds, these observations seem highly indicative of a reproductive cycle in Mourning Doves held captive in Madison closely paralleling that of their wild congeners, free to undertake their annual migrations. Is the annual reproductive cycle an inherent mechanism so deeply impressed on the germ plasm by the regular habits of untold generations of ancestors that it continues to swing through its chronological phases regardless of environmental changes? Or is it, like most physiological processes, conditioned directly or indirectly by some impinging stimulus? A review of the situation eliminated most of the conditions that could be considered seasonally comparable for the two sets of birds. About the only one that remained to which they would be exposed was a change to a longer day in the spring and the reverse of this in the fall. Rowan's results strongly suggested this as a probable controlling factor, and fortunately it was fairly easy to set up a test experiment. Two similar small rooms were accordingly constructed, to be illuminated entirely by artificial light so operated by an electric time switch that the periods of light and darkness could be controlled independently in the two rooms. Other conditions in these rooms are similar and like those in the general loft, that is, they are carried at as near 70° F., or a little above, as possible throughout the winter. Feed and other factors in the management are the same, the only difference being the controlled light periods. These rooms happen to be numbered 201 and 202, respectively, and may be so designated. A single 60-watt Mazda lamp supplies the light in each room.

Into Room 201 were put on November 29, 1930, the two pairs of birds described fully above, namely Mourning Dove female D169.2 and her Mourning Dove mate, D104B, and Mourning Dove male, $D261E_2$, with his Ring Dove mate, D356.5. Two young birds whose sex at the time was unknown, but which turned out later both to be males, were also put in this room.

In Room 202 were installed two Mourning Dove females, each mated to a Ring Dove male, and two young Mourning Doves whose sexes are as yet undetermined. The two females had both laid through the preceding June and July, but gave no fertility.

For about two weeks after the birds were put in, those in both rooms were given 10½ hours (7 A.M. to 5:30 P.M.) of light and 13½ hours of darkness daily. This was taken as being approximately the mid-winter length of day (including half the twilight period) at about latitude 30°, which may be taken to represent roughly the winter range for the species. Beginning with December 11, the daily light period in Room 201 was increased 45 minutes and held so for a week, being then increased the same amount each successive week until February 26, when this room was getting a "day" of 19½ hours. This was taken to represent about the mid-summer effective daylight period at Madison (latitude approximately 43°). The birds in this room therefore experienced from December 11 to February 26 the range of increase in "effective daylight" period that migrating birds would experience from mid-winter in the South to mid-summer in the North. The light period in Room 202 was left constant at 10½ hours throughout.

The results in the case of the two pairs previously discussed are particularly interesting and significant. Thus Mourning Dove female D169.2 had not laid since August 25. For five seasons she had not begun to lay in the spring until early in April (Table I). This season, however, under the conditions of early increase of "daylight" period in Room 201, she laid on February 4 and 5, and again on February 24 and 25.[1]

[1] This bird died March 16, 1932.

The Ring Dove female, D356.5, had been laying fairly regularly up to the time she and her mate were put in Room 201 (see Table II). Her last egg was laid on November 26, three days before they were transferred. On January 20 she resumed laying and the fact that the eggs were fertile, which they had not been since the preceding July, shows that the Mourning Dove male had also resumed reproductive activity.

It will be recalled that the other two Mourning Doves in this room proved both to be males. $D261C_4$ died on February 4 with no previous indication of being sick and no discoverable lesions. The testes at that time had enlarged to medium size and on sectioning showed indication of active spermatogenesis. The other bird, $D261A_4$, was examined by laparotomy on February 10 and the testes recorded as "large."

Of the birds in Room 202, which has remained on the short day, none has laid up to March 15. Two of these female Mourning Doves laid during June and July, 1931. Furthermore, the Ring Dove mate of one of them has shown evidence of reproductive activity by cooing and coaxing the female in normal fashion.

Again, while the number of birds dealt with is small, the results obtained in the "increasing light" room, compared with previous seasons and with the control room, seem fairly conclusive and tend to substantiate the findings of Rowan and of Bissonnette.

Relation to Migration and Distribution.

The suggestion of Rowan that increasing or decreasing day is the indirect stimulus to migration appears very plausible on the basis of the facts so far obtained. Many subsidiary questions remain, however, to be answered. One of these has already been mentioned, namely, what directs the birds on their northward journey in the spring and southward in the fall? This involves the whole question of migration routes, and while there are doubtless general factors involved, the details differ with different species. Before we can expect to solve these problems we shall require much more detailed and exact information regarding individual migrations. Such information is gradually accumulating for a good many species as a result of bird-banding operations.

Another obvious question involves the dispersal of a species over a breeding range covering a latitude almost as wide as its range of migration. Thus the Mourning Dove in the Mississippi valley winters largely in the southern states at a latitude generally below 35° and migrates northward in spring as far at least as Winnipeg, at latitude 50°. Furthermore, it breeds over this entire range from Texas to Canada. The successive fronts (isepipteses)[1] of the northward migration at 10-day intervals are depicted in Chart I, based on records generously furnished by the Bureau of Biological Survey. These records give the average dates of spring arrival of migrating Mourning Doves, over varying periods of years, obtained from observers scattered at numerous points through the Middle States and southern Canada. It will be noted that while there is a successive pushing forward, the front line for any particular date does not coincide with any parallel of latitude, which, with respect to daylight period, would constitute an "isohemer."[2] Instead there is an early advance in the Ohio valley, succeeded by a later acceleration up the valleys of the upper Mississippi and Red Rivers. If the advance of migration is controlled in anything like a mechanical way by the increasing length of day why do not the isopipteses coincide more closely with the isohemeral parallels? But still more strange, why are not *all* the Mourning Doves in the Southern States, say in February, impelled to move northward to Canada with the advancing season?

The answer to the first question is probably involved in that to the second, and an answer to this is suggested by the breeding in captivity of other wild species of doves. It has been observed that the females of a number of species, for example the Damara Dove (*Streptopelia damarensis*) and the Senegal or Palm Dove (*Stigmatopelia senegalensis*), continue to lay more or less regularly throughout the winter months. These are species whose natural

[1] "In aviphenology, an isochrone of the arrival of migrating birds of any given species in the spring. From ἴσος, equal + ἐπίπτησις, a flying towards. A. Th. von Middendorff, 'Die Isepiptesen Russlands,' Mem. Acad. Sc. St. Petersb. 10, pt. 2, 1859, p. 1–143." I am indebted to Mr. C. F. Talman, Librarian of the U. S. Weather Bureau for this reference.

[2] From ἴσος, equal + ἡμέρα, day.

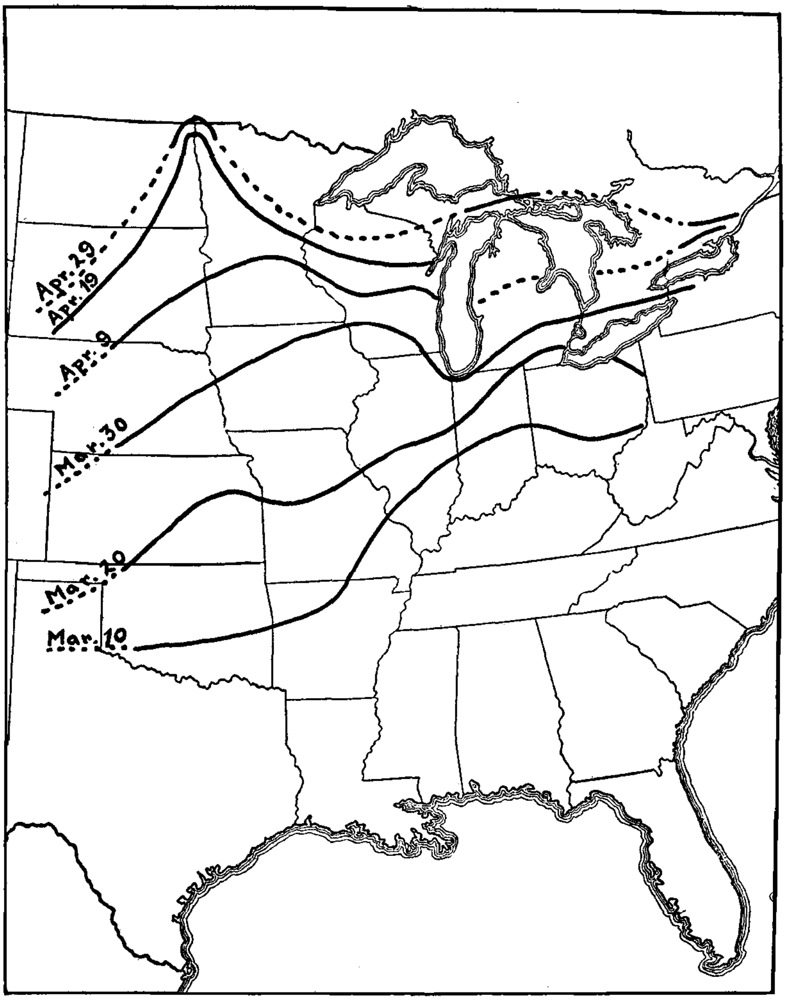

CHART I.—SPRING MIGRATION OF THE MOURNING DOVE.
Average arrival. Based on data from U. S. Biological Survey.

habitat is subtropical and they might be expected, therefore, to be attuned to a shorter day than a bird nesting in the higher latitudes. In other words, there may be a specific genetic difference in the day lengths to which the reproductive organization of different species respond. Is it not possible that, similarly, within the single species of Mourning Doves there may be a genetic differentiation of geographical groups nesting at different latitudes, in the adjustment of their reproductive response to length of day—some attuned to the shorter days of the South and others to the longer days of the North? In the spring migration then, as the bulk of the species begins its northward movement in response to the lengthening days, those birds genetically attuned to a relatively short day would come into reproductive activity, say, in the latitude of Texas or Oklahoma, and would remain there to breed while the others moved on. In the same way, those birds descended from a stock whose summer home was in Kansas or Missouri or Iowa, and which were responsive to the lengths of day in those respective states, would drop out as they reached their own territories, until finally those which were reared in Canada and attuned to the long summer day of the North would push to the northern limit of the range of the species before ending their migration and settling down to nest. Such genetic diversity in the reproductive-light response would not only account for the wide north-and-south summer dispersal, but would also help to explain the nesting of birds in the same regions in which they were hatched, a fact that has been abundantly attested by banding results. The fact that they do tend to nest in the same region would lead to some degree of inbreeding and tend not only to preserve but to strengthen the regional genetic differences.

It is not to be supposed that such a relatively simple hypothesis will account for all the diverse fact of bird migration and distribution, but at any rate it may serve to explain some of the outstanding features. Fortunately it can be put to test, and this it is proposed to do by securing summer-resident birds from the extremes of their range, as well as from intermediate points, and subjecting them to increasing and decreasing light periods under controlled conditions. If the birds from different latitudes are genetically attuned to different day lengths, their response under the experiment should bring the fact out.

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