PHOTOPERIODISM AND MIGRATION

By MARIE ROLLO

MANY theories have been advanced for the migration of birds but each of these is open to objections. While one factor may seem to control the migration of several species it breaks down when applied to others. This has led to the assumption that migration is an inherited instinct and is performed now by birds without any evident stimulation, and that the original causes for migration were not the same for all species (Lincoln, 1939). However, there is so much regularity, at least in true north and south migration, that it seems that one factor in the environment must be responsible, or, at least, supreme in stimulating the predictable arrival and departure of birds. If several factors were involved or if there was no active stimulation there would not be as much of a pattern in the migratory movements of all birds. An acceptable theory must hold for all species and for all details, and in meeting these requirements, of all the theories advanced, the one of photoperiodism seems to offer the most hope.

Eifrig (1924) was the first to point out that the gradual change in daily light period was the only environmental factor that varied regularly enough to account for migration, but many authorities have not given this theory much weight. Among their objections are the following: Trans-equatorial migrants commence their northward journey while the days are actually decreasing in length. Some birds leave for the south when the daylight is still increasing and the longest day has not been reached. Rowan found that northward migration was the result of stimulation of the gonads by gradually increasing light periods but Bissonnette called attention to the fact that birds often reach their breeding grounds before their gonads are fully distended. It may be that we have not had a clear understanding of how a bird responds to this factor of the environment. Many experiments have been done recently in the field of photoperiodism by the botanists and zoologists from which a few simple principles can be drawn which will provide us with a framework that will explain these seeming inconsistencies and make these objections disappear. Rowan (1925) demonstrated that increasing daily light periods stimulated enlargement of the gonads and northward migration. Bissonnette (1930) confirmed this stimulatory action, and demonstrated the effects of various intensities and wave-lengths. Benoit (1936) and others have shown that light is effective through the hypophysis and that the hypophysis in turn stimulates the gonads. Garner and Allard (1920) have shown that plants respond to a daily light period which varies with the species and sometimes with the variety, and that

this response is inherited in the germ plasm and is passed on in the regular Mendelian way in hybrids.

In my own experiments (Brown and Rollo, 1940, and other experiments, unpublished) on weaver finches (*Pyromelana franciscana*) increasing the daily light period gradually was not as effective in producing the nuptial plumage as giving them optimum daily light period from the start. When weavers received ten, eleven, twelve, thirteen, fourteen, sixteen and eighteen hours of light daily, those on a thirteen and fourteen-hour period came into color first. An eighteen-hour period retarded the appearance of nuptial plumage as much as an eleven-hour period. At nine hours, they remained in eclipse plumage.

Paradise whydahs (*Steganura paradisaea*) assumed nuptial plumage on a twelve-hour period, but went into eclipse plumage on both a ten and a sixteen-hour period. A daily light period above as well as below the optimum did, not only, not stimulate but actually retarded the appearance of nuptial plumage. Each of three genera used responded to a different optimum daily light period. On dissection a correlation was found between the state of the gonads and the appearance of nuptial plumage, so that nuptial plumage can be taken as an indication of sexual activity in this species. The following principles might be drawn from these experiments and applied to migration:

1. Plants and animals inherit their ability to respond to a certain daily light period.
2. The optimum period varies with the species and sometimes with the variety.
3. Optimum period is more effective than gradually increasing and decreasing light periods.
4. Too long a period makes for regression as well as too short a period.
5. Light is effective through the hypophysis.

Birds in their response to light can be compared to plants. In the first stage of a plant's life, humidity and temperature are most important, and this is true in a fledgling's life. From the appearance of the first shoot in a plant, to the reproductive stage, however, light is of utmost importance, and temperature and humidity are only secondary. This is true of birds in the same stage. Bissonnette has shown that it is not the extra food consumption but the effect of the light itself that stimulates reproductive activity. Bishop weavers on a fourteen-hour light period can go for forty-eight hours without food and show no ill effects but will starve to death in four and a half hours on a nine-hour light period.

There is this difference between birds and plants: plants without optimum daily light period fail to mature and reproduce, while birds, with their ability to travel, migrate to where they can get

optimum period. As in plants, the optimum period varies with the species and variety, and the length or migration in birds varies accordingly. As a general rule long-day plants are found in the extreme north and the equivalent in birds is found in the Arctic Tern which migrates from the Arctic to the Antarctic. Near the equator we have the short day and ever-blooming type of plants, and we have birds that migrate just a few degrees and some that breed throughout the year. Bishop weavers and whydahs that ordinarily have a seasonal change of plumage have, in my experiments, been kept in nuptial plumage for almost two years on an optimum light period and can be compared with the everblooming type of plant.

Bissonette and Rowan have already shown that increase and decrease in daily light period need not correspond with that in nature. If we now consider that it is not this increase and decrease in period that stimulates birds to migrate but a search for optimum period, we can understand why trans-equatorial migrants commence their northward journey while the days are decreasing in length. They migrate to the latitude that has a light period to which they have inherited the ability to respond. Too long a light period made for regression in my experiments. This will explain why birds sometimes leave for the south when the daily light period is still increasing and the longest day has not been reached in the north because the longer light period is above the optimum for their need at that time. The fact that light is effective through the hypophysis instead of the gonads explains why birds often reach their breeding grounds before their gonads are fully distended, for while the gonadal development is part of the picture it is probably not the means of control of migration. A correlation is found between plumage changes, migration and reproduction. If the hypophysis controls reproduction and plumage changes it seems reasonable to assume that it is also the means of control of migration.

Other factors enter into migration but not in a haphazard way. Light period comes first. Moreau has pointed out that birds migrate south over the Sahara desert in a straight line and in equal numbers across its entire breadth, and that they may be found in hundreds, starved to death, not being able to reach the other side, but they do not follow the Nile where food and water are available.

From this point of view, the theory of photoperiodism seems to hold for all species in their true migration.

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NEW BIRD-TRAPPING DEVICES

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THE devices hereinafter described have provided efficient methods of capturing birds of various kinds for the purpose of studying the ectoparasites with which they are infested and also for determining the extent to which they serve as intermediate hosts for parasites of domestic animals. It is believed that the devices will be useful in other biological studies where the trapping of birds is necessary.

MODIFIED "FIGURE 4" BIRD-TRAP TRIGGER

The usual "figure 4" bird-trap trigger has a number of undesirable features, especially when the traps are used extensively. First, the single vertical post of the trigger is an inadequate support for the trap and other trigger parts. The support is not steady enough to prevent the trap from slipping or falling, especially in a strong breeze. Second, the base of the post, which is usually small, sinks, especially if the ground is soft. Here again the trap may be sprung, or the trigger rendered inoperative. Last, and most important, the trigger bar of the ordinary "figure 4" trigger is not equally sensitive to light pressure from all directions.

The improved trigger was designed to remedy the above-mentioned faults. The single support post of the usual type is