

## THE ANNUAL STIMULUS FOR MIGRATION

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Among the fascinating aspects of bird migration are its cyclic nature and its temporal precision. Twice annually, in a migratory species, there must be some type of stimulation which causes the development of the complex migratory behavior pattern. It is the purpose of this discussion to present an inventory of our knowledge concerning the nature and mechanism of this periodic stimulation. For present purposes, migration is defined as a regular, usually annual, movement of at least a portion of the population of a species from the breeding area to a non-breeding area, and a return of at least a portion of the individuals to the breeding area. It is definitely oriented and periodic but is not necessarily to be implied to "involve reproduction" as suggested by Gadow, BULLOUGH, Rowan, and others. Care must be exercised in excluding, as non-migratory, many so-called vagrant and sporadic movements; some of these may represent initial phases in the development of more typical migratory movements or modifications of more typical migratory patterns. The traditional German designation (Weigold, 1924, and others) of "instinct" and "weather" migrants likewise should be applied with caution since the establishment of distinct differences is difficult in many instances. The latter could in some instances represent a developmental stage of the former.

With their aerial mobility, high metabolic rate, and relatively highly developed instinctive behavior, birds are perhaps the best equipped, among all groups of animals, for the development of migratory behavior. Because of these "preadaptions" for migration and further because of the peculiarly scattered distribution of migratory habits among the families and orders of birds, it appears not unlikely that migratory behavior may have evolved several or many times in the course of the evolutionary history of modern birds and that, in studying migration, we may actually be confronted with many subtle cases of convergent evolution. This in turn may mean that the selective processes, the stimulatory mechanisms, the mechanisms of navigation and orientation, and other aspects of migration could be different in different species.

With this suggestion in mind, it may be pertinent to present a few remarks concerning some of the pitfalls associated with the interpretation of experimental data and observations relating to migration in general and to the stimulation of migration in particular. (1) *The tendency to regard all migration as having a common origin, or at least, as the result of the same factors.* This assumption may be true but the available evidence, at present, generally indicates it to be improbable. There seems to be no common denominator in migration other than migration itself. (2) *The rather frequent tendency to transfer conclusions concerning one species into explanations concerning other species and to construct general theories based on evidence from one or a few species.* This is a corollary of 1. In some instances transfer may be valid; likewise in many instances it is not. (3) *Confusion of correlation with cause and effect.* This is not an uncommon difficulty in many fields of biologic investigation. Usually this has involved the assumption that in a correlation between two phenomena one must be cause and the other effect, whereas in reality both may be the effects of an undetected cause. An example in migration may well be the correlation between migration and the reproductive cycle such as in the recrudescence of the gonads. (4) *Excessive generalization.* Few experiments and observations concerning bird migration have true statistical reliability. Most data and observations in this field are, from the standpoint of the entire field, suggestive rather than definitive for purposes of generalization. Experiments which will yield significant data are difficult to plan and execute.

Two periods may be recognized in the history of our knowledge of the annual stimulation of migration.

The period of observation (1825-1925) is characterized by theories, usually unifactoral, based solely, or at least largely, on uncontrolled observations. Many of the theories bestowed on birds untenable attributes such as intelligence and ability to plan. Many confused the factors of annual stimulation and the selective factors which fix the response mechanism although it must be admitted that, in some instances, these may be closely related. The hypotheses and theories proposed during this period, in one way or another, have suggested, implied, or anticipated, most of the factors and ideas of our current concepts. As a rule, however, these theories were generalized from restricted observations, and although frequently proposed as general theories, they failed to have general application. Among the stimuli or causes suggested for migration were changes in temperature, changes in rainfall, changes in atmospheric pressure, changes in humidity, changes in food supply, urge to reproduce, urge to return to ancestral home, seeking of additional space for reproductive activities, freezing of lakes and streams, seeking of traditional nesting habitat, and "following the course of the sun." Although some important concepts were introduced, many of them passed unnoticed. The important contributions of this period are aptly summarized by Wachs (1926).

The experimental period, which is characterized by the combination of observational and experimental approaches to the problem of the annual stimulation of migration, began with the first experiments with Slate-colored Juncos (*Junco hyemalis*) in Alberta by Rowan (1925).

In these pioneer experiments (Rowan, 1925, 1926, 1929, 1931, 1946) juncos were subjected in winter to artificially increased day lengths. The testes of these birds gradually increased in size whereas in the controls the testes remained at a size normal for the season. Rowan associated the increasing size and development of the gonads of the experimental birds with the similarly increasing size and development in spring migrants. When light-treated birds were released in mid-winter, many disappeared whereas controls with undeveloped gonads remained in the vicinity. This was interpreted as an indication of migration on the part of the experimental birds.

Further experiments by Rowan (1928) on the mechanism by which increased day length caused development of the testes have led to an interesting ramification. He concluded that, in the experiments involving increased day length in juncos, a more direct cause of the increase in size and development of the testes was actually an increase in exercise. Bissonnette (1930, 1931a, 1931b, 1933) was unable to reach a similar conclusion from experiments with Starlings (*Sturnus vulgaris*). However, the extreme nervousness and restlessness of the experimental birds seems to preclude significant conclusions. Rowan (1937, 1938) contested Bissonnette's experimental results principally on the basis of observations that Starlings in London subjected to traffic disturbances but only slight increase in light showed earlier recrudescence of gonads than Starlings in the quiet suburbs. On the other hand Bullough and Carrick (1939), and Bullough (1942a, 1942b, 1945) have assembled a rather convincing body of data which indicate that Rowan was actually dealing with two physiologically distinct races.

Experiments on migration were also conducted with Crows (*Corvus brachyrhynchos*) by Rowan (1930, 1932, 1946). In winter releases of Crows, which had been subjected to artificially increased day length, some northwesterly movements were obtained; there were also southeasterly movements; also some individuals were sedentary. Castrates, similarly treated and released, with a single exception (described as a partial castrate) were sedentary or moved in a southeasterly direction. Non-castrate controls which received no light treatment were sedentary or moved in a southeasterly direction

typical of the normal migration in autumn. These results appear to indicate the necessity of the testes in the stimulation of northward migration. Schüz (1948) interprets them as indicating that both the gonads and anterior lobe of the pituitary gland are necessary. Experiments involving treatment with certain hormonal preparations were inconclusive.

Rowan (1926, 1929) first proposed that migration, spring or fall, is stimulated by hormones secreted by the testes or ovaries at a certain stage of partial development and that the regression and recrudescence of the gonads is caused by the decrease and increase in day length in spring and autumn. Later, in consideration of the results from the experiments with Crows, Rowan (1931, 1932) revised his theory to the effect that fall migration is probably not dependent on any particular stage of regression but only on regression, castration representing the maximum regression. Still later, Rowan (1946), although still placing emphasis on the role of the gonads, suggested that the pituitary gland and "the entire physiology of the animal" are involved in the stimulation of migration. Previously Cahn (1925) and Bergtold (1926) had suggested a causative relation of the vernal development of the gonads to the annual stimulation of spring migration.

Schildmacher (1933, 1934a, 1934b) has reported results from experiments on young and adult European Redstarts (*Phoenicurus phoenicurus*); these data have been interpreted (Bullough, 1945) as support for Rowan's theory of a gonadal stimulation of migration. It was reported that small injections of female sex hormone caused a cessation of migratory behavior in fall in caged birds, whereas migratory behavior persisted when larger injections were made. Schildmacher, in interpreting these results, assumed that fall migration is the result of decrease in sex hormones, whereas spring migration is stimulated by an increase in sex hormones. He then suggested that the small doses counteracted the stimulating effect of decreasing sex-hormone level whereas the large doses actually produced a simulation of springtime migratory behavior. These experiments have been criticized, with apparent justification, on several points by van Oordt (1943), Steinbacher (1933), and Desselberger and Steinbacher (1934). Stadie (1938, 1939) likewise was unable to confirm Schildmacher's results with similar experiments on the Redstart, although previously Giersberg and Stadie (1934) had reported the release of migratory behavior (*Zugunruhe*) with injections of female sex hormone in a male Whitethroat (*Sylvia communis*) and in a male Lesser Whitethroat (*Sylvia curruca*). Merkel (1938) suggests that Schildmacher's results were the consequence of increased metabolic rate.

Schildmacher (1937, 1938b) demonstrated, with limited numbers of European Robins (*Erithacus rubecula*) and Redstarts, premature recrudescence of gonads and migratory behavior in caged birds (*Zugunruhe*) with artificially increased day lengths. The results with Robins have been confirmed by Putzig (1937, 1938c). As indicated subsequently, these data need not necessarily be interpreted as indicating a cause (gonadal recrudescence) and effect (migratory behavior) relationship.

Rowan's gonadal theory of the annual stimulation of migration has been accepted in its general aspects in a recent review by Bullough (1945) as a basis of the difference of migratory status between the British and continental Starlings. Lincoln (1935) also suggested that migration was caused by physiologic stimuli associated with the reproductive period.

At this point it seems pertinent to enumerate, with brief comments, certain considerations which collectively appear to make improbable any theory of annual stimulation of migration based on the gonads as the immediate stimulators of migratory behavior.

These considerations are in addition to certain technical criticisms by Wolfson (1940, 1941).

(1) Transequatorial migration virtually precludes a simple general application of Rowan's theory of photoperiodism operating through the gonads as well as any theory based fundamentally on simple photoperiodism. Rowan (1926) recognized this difficulty and suggested that the pattern of migration may become sufficiently fixed, according to the light conditions of the northern hemisphere, so that the excursion into the reversed conditions of the southern hemisphere would have no effect on this established pattern. Moreau (1931) in a critique of Rowan's theories concludes that his suggestion of the fixation of a pattern in accordance with light patterns in the northern hemisphere is the only plausible explanation. Moreau suggested the possibility that simple response to photoperiodism represents the primitive condition in migration and that a pattern independent of photoperiodism, such as required in part by transequatorial migrants, represents a more highly evolved situation.

(2) The necessary assumption of similar (or identical) functions of the ovaries and testes, or the assumption of very similar (or identical) functions of male and female sex hormones, although not impossible, is difficult to accept.

(3) The experimental data of Rowan (1925, 1926, 1930, 1932), Schildmacher (1937, 1938*b*), and Putzig (1937, 1938*c*) show, under conditions of artificially increased day lengths, simultaneous recrudescence of the gonads and development of migratory behavior. This is also a commonly observed correlation under conditions of naturally increasing day length. These data and observations are interpreted in the gonadal hypotheses of the annual stimulation of migration as a matter of cause (gonadal recrudescence) and effect (migratory behavior). Actually, with the possible exception of the data on the light-treated castrated male Crows obtained by Rowan (1932), these data could be interpreted in terms of two effects (gonadal recrudescence and migratory behavior) resulting from a more profound cause such as possible changes in the anterior lobe of the pituitary gland in response to changing conditions of light. Cole (1933) in discussing data on the reproductive cycle of the Mourning Dove (*Zenaidura macroura*) noted that whereas it should be reasonable that there be some causal connection between annual migration and the reproductive cycle, "there has been disagreement as to which was cause and which effect."

(4) There has been a slow accumulation of records of castrated males which migrated both in spring and fall. However, only spring migration by castrated males can be construed as contrary to Rowan's (1926, 1932) theory. Such cases have been reported by Putzig (1938*c*) for five Hooded Crows (*Corvus cornix*), Hann (1939) possibly for a Red-eyed Towhee (*Pipilo erythrophthalmus*), Drost (1941) for a European Blackbird (*Turdus merula*), Emlen (Wolfson, 1942:260) for three Gambel White-crowned Sparrows (*Zonotrichia leucophrys gambeli*). This type of evidence is actually not as completely contradictory as might appear initially. Hooker and Cunningham (1938) have reported that the testes can regenerate occasionally in castrated male domestic fowl. Whether or not regeneration was actually from somatic tissue is immaterial in the evaluation of castration experiments on migration. Also it is possible that castrates without migratory urge might still accomplish migration in association with a flock of normal birds. Nevertheless, migration of castrate males does weaken the idea that the gonads are primarily involved in the annual stimulation of migration.

(5) Certain of the experimental data obtained by Wolfson (1940, 1941, 1942, 1945) are interpreted by him as contrary to the gonadal hypotheses. In experiments with Oregon Juncos (*Junco oreganus*) it was found that migration occurred in birds held in spring until gonads were at maximum size and development hence indicating, in this

species, that a certain developmental stage is not the requisite condition for migration. Injections of Antuitrin G (primarily somatotrophic hormone) caused recrudescence of the gonads as well as the deposition of fat, the latter being regarded by Wolfson and others (Merkel, 1937, 1938) as a requisite condition for migration. Gonadotropic hormone preparations (pregnant mare serum and chorionic gonadotropin plus follicle stimulating hormone from the anterior lobe of the pituitary gland) caused recrudescence of the gonads but not deposition of fat. This was interpreted (Wolfson, 1945) as an indication that the sex hormones from the developing gonads cannot cause the deposition of fat which characteristically precedes migration. It is interesting to note, on the other hand, that estrogens, natural and synthetic, can cause fat deposition in both sexes (see, for example, Bird, 1946). This could not, however, account for a premigratory deposition of fat in males.

(6) As has been pointed out by Eifrig (1924), Stresemann (1934), and others, some migrants complete spring migration before there has been much, if any, development of the gonads; in such species a gonadal stimulation of migration seems improbable. Rowan and Batrawi (1939), however, have presented data on small numbers of six European migrants at the beginning of northward migration in Africa in spring; all showed the beginning of recrudescence.

(7) Sedentary species and races frequently have the same gonadal cycle as closely related migrant forms (see, for example, Wolfson, 1942, 1945, and Blanchard, 1941, on *Junco oreganus* and *Zonotrichia leucophrys*, respectively).

(8) Further it seems improbable that the profundity and temporal pattern of the physiologic changes which have been associated with migration by Groebels (1928, 1930, 1932), Merkel (1937, 1938), and Putzig (1939) could be based primarily on the gonadal cycle.

In view of these considerations in their entirety, it does not seem justifiable to accept a general hypothesis of the stimulation of migration in which the gonads are assumed to have a generally direct, fundamentally stimulatory role. This is not meant necessarily to rule out a contributory role by the gonads under the influence of the anterior lobe of the pituitary gland, nor to disregard them as an essential part of the stimulatory mechanism in certain species, as suggested by the failure of Rowan's light-treated castrated Crows to develop reverse migration in autumn. Putzig (1938c) has speculated on the possible interrelationships of the anterior lobe of the pituitary, thyroid gland, and developing gonadal tissues in the stimulation of spring migration. It seems not impossible that the role of the gonads in migration may differ in different species. For the present, we must continue to note that most of the evidence does not necessarily support, and some actually denies, a simple primary stimulatory role on the part of the gonads.

At this point it appears logical and desirable to discuss briefly a phase of the investigation of the physiology of migration which has received considerable attention in Europe. This is the investigation of *Zugunruhe* which is the restlessness displayed by caged migratory birds during the migratory period. It is assumed, with apparently good evidence, that the physiology of *Zugunruhe* is a reasonable representation of the physiology of migration; consequently the investigation of *Zugunruhe* has been used as a tool in the study of the annual stimulation of migration. The phenomenon of restlessness on the part of caged birds during the normal migratory period apparently has been well known for a long time. For example von Homeyer (1881) cites Naumann's (1822) description of it in caged Nightingales (*Luscinia megarhyncha*) in February. *Zugunruhe* was also known to Palmén (1876); Wachs (1926) states that it was described in some detail by Eckström in 1828. However, the initial significant investigations were

those of Wagner (1930) who recorded the activities of Whitethroats, European Robins, Bluethroats (*Luscinia svecica cyaneocula*), Song Thrushes (*Turdus philomelos*), European Blackbirds, and Redwings (*Turdus musicus*); it was noted that this restlessness in caged birds corresponded fairly closely in daily and annual patterns to natural migratory behavior, although the spring period of *Zugunruhe* extends longer than the spring migratory period.

In later papers (Wagner, 1936; Wagner and Schildmacher, 1937) data were presented on the development of *Zugunruhe* in passerine birds transported out of their normal range. Also Wagner (1937) presented data interpreted as indicating that the development of *Zugunruhe* during the migratory season is somewhat dependent, varying with the species, on the amount of food available; in Song Thrushes, low temperatures appeared to be stimulatory or augmentatory. In Robins and Whitethroats it was found that intensity of light in the experimental room at night was an important factor. Numerous investigations have been made (Ahlquist and Palmgren, 1935; Palmgren, 1937, 1938, 1943, 1944a; Siivonen, 1936; Siivonen and Palmgren, 1936) concerning causal and modifying factors as well as of the fundamental patterns of *Zugunruhe* in the European Robin, Garden Warbler (*Sylvia borin*), and other species. The data therefrom suggest that *Zugunruhe* is the expression of fundamental physiologic factors although environmental factors may have important stimulating, inhibiting, or modifying roles.

Investigations by Merkel (1937, 1938) on Whitethroats, European Robins, and other species have made noteworthy contributions to the physiology of *Zugunruhe*. It was concluded that *Zugunruhe* is dependent on two physiologic phases: (1) *Zugdisposition* characterized by increased food intake and changes in metabolism, such as decreased metabolic rate, resulting in an accumulation of fat and, probably more important, the ability to replenish rapidly the weight (primarily fat) lost in periods of *Zugunruhe*, or presumably in actual migration, and (2) *Zugstimmung*, the actual process of migration, expressed as *Zugunruhe* in caged birds, which the author presumed to be initiated by increased secretion of thyroid hormone which mobilizes energy-rich reserves. Temperature was found to be an important modifying factor both in the appearance of and in the intensity of *Zugunruhe*. Recorded *Zugunruhe* has been the source of the basic data in the previously cited experiments of Schildmacher (1933, 1934a, 1937, 1938b), Stadie (1938, 1939), Giersberg and Stadie (1934), and Putzig (1937, 1938c). The phenomenon of *Zugunruhe* has been reviewed briefly by van Oordt (1943) and more extensively in an excellent treatise by Palmgren (1944b). The latter suggests that the daily and annual activity patterns, of which *Zugunruhe* and, presumably, natural migratory activity are a part, are the result of a number of component activity rhythms which, from time to time, differ in the degree of synchronization.

Several investigators have considered changes in the activity of the thyroid gland as integral or fundamental in the annual stimulation of migration. Wagner (1930) in his investigations of turdid species and Whitethroats was able to produce a simulated *Zugunruhe* with injections of thyroxin. Riddle, Smith, and Benedict (1932) in comparing the physiology of metabolism of the migratory Mourning Dove (*Zenaidura macroura*) and the non-migratory common pigeon suggested that migration in the former may be explained by failure of the thyroid gland in this species to respond to colder weather by increased activity, thus necessitating a movement to a warmer area. This conforms with data presented by Riddle and Fisher (1925) and in part with that of Häcker (1926) and Watzka (1934) which are interpreted as indicating that the thyroid glands of some species of birds may become more active during colder temperatures. Kendeigh (1934) has discussed this suggestion in relation to a comparison of the mi-

gratory House Wren (*Troglodytes aëdon*) and the non-migratory English Sparrow (*Passer domesticus*).

Merkel (1937, 1938) was able to produce *Zugunruhe* in Whitethroats and European Robins in *Zugdisposition* with small injections of thyroxin or thyrotropic hormone; large doses of thyrotropic preparations interrupted *Zugunruhe*; Merkel suggested that the thyroid gland has an integral function in the annual stimulation of migration; he found his data and conclusions to be in agreement with the concepts of cyclic thyroid physiology in some species as proposed by Häcker (1926), Kückler (1935), and Elterich (1936). Merkel suggested further that the difference in thyroid activity required for migration and molting makes these two processes, in general, mutually exclusive. Putzig (1938*b*) does not share this opinion, indicating several exceptions. Merkel's hypothesis is contrary to the thinking of Groebbels (1930) who suggests that the fat accumulation characteristic of *Zugdisposition* is attained by decreased dissimulation due to reduced endocrine function of the gonads and thyroid gland.

Putzig (1938*b*), with reference to his investigations of Lapwings (*Vanellus vanellus*) and other limicoline species, reached the conclusion that the thyroid gland, because of its role in regulation of metabolism, must have a significant role in migration. His data from histologic studies of the thyroid glands of the above-mentioned limicoline species seem to indicate some correlation between migration and resorption of colloid from the follicles; however, the data are by no means conclusive.

Experiments with European Robins involving injection of thyrotropic hormone were reported to cause simulated or enhanced *Zugunruhe* in birds in *Zugdisposition*. Putzig was unable to confirm Merkel's (1937, 1938) experiments in which an excess of thyrotropic hormone was found to inhibit *Zugunruhe*. Later, in considering results of his experiments on castrate migrants, Putzig (1939*a*, 1939*b*) obviously thinks of the role of the thyroid as a part of a more intricate endocrine and metabolic pattern in the stimulation of migration.

Although the investigations on the role of the thyroid gland in the stimulation of migration are fragmentary, indecisive, and the source of contradictory hypotheses, there seems, especially in view of the known functions of the thyroid hormone and its control by the thyrotropic hormone of the anterior lobe of the pituitary gland, to be considerable probability that the thyroid gland is, in some way, an integral part of the mechanism which stimulates migration. A positive interpretation of this role of the thyroid gland should involve a repetition and extension of many of the previous investigations in light of recent investigations and interpretations of thyroid function (see, for example, de Robertis, 1949), and a consideration of the role of the thyroid gland in the more general metabolic and endocrine aspects of the problem.

A general metabolic basis for migration has been suggested or discussed by Groebbels (1928, 1930, 1932), Merkel (1937, 1938), Putzig (1938*a*, 1938*b*, 1939*b*), Ken-deigh (1934), van Oordt (1943), and Wolfson (1942, 1945). Actually Rowan (1926) and Wachs (1926) have anticipated these suggestions; the latter proposes a special metabolic condition which recurs twice annually. Rowan's suggestion involves a possible interplay of several endocrine organs.

(A careful consideration of the available information, experimental and observational, on the annual stimulation of migration seems to lead invariably to the conclusion that associated with the premigratory period, and apparently prerequisite to migration, are certain fundamental changes in metabolism, often reflected as fat deposition during these periods. To trace the history of the knowledge and recognition of the association of fat deposition with the beginning of migration as well as the association of fat deposition with certain fundamental changes in metabolism is difficult. According to

Wachs (1926) Naumann in 1822 associated fat deposition with the beginning of fall migration.

Zedlitz (1926) analyzed somewhat fragmentary data on monthly variations in weight for certain central European migrants, permanent residents, and winter visitants. He noted that winter visitants, such as the Brambling (*Fringilla montifringilla*), Fieldfare (*Turdus pilaris*), and Bohemian Waxwing (*Bombycilla garrulus*) arrived in fall in fat condition; considerable variation occurred through the course of the winter. The data on permanent residents such as the Magpie (*Pica pica*), the Yellow-hammer (*Emberiza citrinella*), Willow-tit (*Parus atricapillus borealis*), and the Marsh-tit (*Parus palustris palustris*), although very fragmentary, indicate a fairly constant maintenance of weight, through the course of the winter, with some fat deposition. Among migrants, Hooded Crows (*Corvus cornix cornix*) were found to be heaviest in spring; Chaffinches (*Fringilla coelebs*) arrived in good condition in spring, lost weight in summer, and almost recovered spring weight in fall; Woodcocks (*Scolopax rusticola*) likewise lost weight in summer and displayed a marked increase in fall.

Groebbels (1928), in discussing the accumulation of fat in fall in migratory species, suggested that it was the result of sort of a physiologic castration and that it might serve as an energy reserve for migration. Although the empirical observations are important, the suggestions as to the cause and functions of such depositions appear rather speculative. Groebbels also noted the arrival in spring of birds with well developed testes and persistent depositions of fat. He (1930) later presented further data on fattening in fall, before or during migration, in a number of European migrants based to a great extent on the data of Weigold from Helgoland. Still later (1932) he presented monthly data on three male Chaffinches, one of which lived three years. Fat deposition occurred approximately during both the spring and fall migratory periods.

Linsdale and Sumner (1934a, 1934b) have published extensive data on the Golden-crowned Sparrow (*Zonotrichia coronata*) which indicate a pronounced increase in weight prior to spring migration. Wolfson (1945) has shown this increase to be the result of deposition of fat. The same phenomenon appears to be indicated by similar data (Linsdale and Sumner, 1934b) for the Fox Sparrow (*Passerella iliaca*) and Wolfson (1945) interpreted their data as consistent with those on the Golden-crowned Sparrow. Merkel (1937) has recorded observations on Whitethroats and other species in which marked increases in weight prior to the migratory period were noted. Baumgartner's (1938) excellent study on the Tree Sparrow indicates weight maxima prior to and during fall migration, in midwinter, and at the beginning of spring migration. Putzig (1939b) in reviewing the metabolic physiology of migration has regarded a premigratory increase in weight as part of the normal physiology of migration.

Blanchard (1941) has found in the migratory Puget Sound White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*) that there is a marked deposition of fat before departure in spring; this deposition of fat apparently is lost by the time the birds reach the breeding area. Wolfson (1945) has added details for this subspecies by the presentation of monthly weight data. A similar weight pattern is lacking in the non-migratory Nuttall White-crowned Sparrow (Blanchard, 1941). Wolfson's (1940, 1942, 1945) observations on the migratory races of Oregon Juncos under both experimental and natural conditions in California indicate clearly an increase in weight because of fat deposition prior to migration. This does not occur in the non-migratory Point Pinos Oregon Junco (*Junco oreganus pinosus*); Wolfson feels that this is typical of sedentary forms in general. Höhn's (1947) data on sedentary Mallards (*Anas platyrhynchos*) agree with this proposition. Kirkpatrick (1944) found that female pheasants (*Phasianus colchicus*) increase in weight in spring; there was no corresponding increase in

males. These data are similar to those of the annual weight curves (Wilson, 1911) of the Red Grouse (*Lagopus scoticus*) in Britain. Conceivably this situation, which may be common among non-migratory species, could be the result of increased estrogen production by the females in spring and may represent quite a different situation than in migratory species in which weight increases occur in both sexes and therefore may not be inconsistent with Wolfson's hypothesis.

Grote (1943) has stated that Longspurs (*Calcarius lapponicus*) arrive on the tundra in spring in fat condition. Dr. Irvin O. Buss (personal communication) has informed me that Upland Plover (*Bartramia longicauda*) in Wisconsin are lean on arrival in spring and fat on departure in late summer.

Nice's (1937) very extensive data on the Song Sparrow (*Melospiza melodia*) in Ohio, however, do not conform with the general pattern for migratory species as suggested by Wolfson. Wolfson (1945) has suggested that this may be the result of the failure to separate resident and migrant individuals. Nice (1946) has consequently re-analyzed and published her data in accordance with migrant and resident status. The data on winter visitants do not indicate a correspondence with the weight cycle in the migrant races of the Oregon Junco and the White-crowned Sparrow in California. Nice (1946) has suggested that climatic differences between Ohio and California may account for the differences. It seems equally probable that fundamental physiologic differences between the species may be involved.

The extensive treatise on bird weights by Baldwin and Kendeigh (1938) like that of Nice (1937, 1946) does not support a general theory of weight increase and fat deposition prior to spring migration. Wolfson (1945) has suggested that this, in part, is because of the failure of the authors to treat the data from the standpoint of migratory status. Whereas this is partially true, a cursory examination of the data of Baldwin and Kendeigh from the aspect of migratory status, in some cases, suggests that such a premigratory increase occurs in weight in spring whereas in others it does not. In general, from this aspect, the data are inconclusive. More recently in Belgium, de Bont (1947) has demonstrated with Chaffinches, as has Wolfson for Oregon Juncos, that increasing the period of exposure to light resulted in fat deposition in migrant birds but failed to do so in non-migratory individuals. Among Wood Pigeons (*Columba palumbus*) and Stock Doves (*Columba oenas*) in spring, de Bont noted two groups, lean birds with well-developed gonads and fat birds with poorly developed gonads; he assumed these groups to be respectively, in each species, the sedentary breeding population and the migratory population which does not breed in Belgium. Wolfson (1945) has discussed, in relation to migration, other published studies of annual weight pattern. Odum (1949) has recently presented extensive data on the weight of White-throated Sparrows (*Zonotrichia albicollis*) taken in the winter range in Georgia. Two peaks, one in mid-winter and a second just prior to northward migration, are evident.

A careful consideration of the available information can only lead to the conclusion that, in some migratory forms, there is certainly a premigratory weight increase resulting from fat deposition and that in some non-migratory species or populations this pattern does not occur. Obviously there is need for extensive year-around weight studies, both of captive birds and of birds under natural conditions, such as that of Baumgartner (1938) on the Tree Sparrow. For the present it seems best to assume that the annual stimulation of migration is dependent on the development of a particular physiologic status which may result in, or be accompanied by, the deposition of fat, or which allows a rapid recovery of weight lost in migratory activity. This may be identical with, or at least contributory to, the condition designated by European investigators as *Zugdisposition*, the condition in which the migratory bird is susceptible to stimulation to

migrate (van Oordt, 1943). Vleugel (1948) has recently suggested that this condition may persist throughout the winter in certain species.

Some information is available concerning other aspects of *Zugdisposition* on the basis of suggestions by Groebbels (1928, 1930, 1932) and Merkel (1937, 1938). Among other things, these investigators have pointed out, in the passerine species studied, that in addition to the premigratory accumulation of fat, there is during the migratory period a marked ability to restore fat deposits without apparent increases in food intake. Groebbels has suggested that this ability to store fat is the result of decreased dissimilatory activity of the thyroid gland and gonads and consequent lower metabolic rate. Groebbels has reported lower body temperatures from migrating birds which have flown into the lighthouse at Helgoland. Whether this is characteristic of *Zugdisposition*, or develops after migration has begun, is not clear. The changes in the daily activity curves preceding, or at the beginning of, the migratory period, described by Palmgren for caged passerine birds may be regarded as a behavioristic expression of *Zugdisposition*. Groebbels (1928, 1930, 1932), Kendeigh (1934), Merkel (1937, 1938), and Putzig (1939) have discussed possible relations of metabolism, nutrition, reflex reaction to reduced food intake and hunger, reduced environmental temperature, and shorter days in relation to fall migration. Particular attention has been given metabolic unbalance resulting from lower food intake relative to energy demands and an automatic readjustment thereto in the form of migration. Obviously other factors would have to be involved in spring migration. Merkel (1938) has suggested that consideration be given in addition to reproductive urge (*Bruttrieb*) and homing sense (*Heimfindesinn*). In general these suggestions are highly conjectural. Much research, including investigations of the activities of the pituitary, thyroid gland, and gonads, must be accomplished before the complex metabolic changes of *Zugdisposition* are understood.

Another aspect of the metabolic basis of the stimulation of migration has received the attention of Kendeigh (1934, 1941, 1944, 1945 and 1949) and Siebert (1949). Briefly, particular attention has been given to existence energy, which includes the energy required for basal metabolism, chemical heat regulation, procurement of food and water, and the "specific dynamic action" of digestion and assimilation, and productive energy, which is the energy available above the requirements for existence at a minimum level of activity and which may be used for such activities as molt, reproduction, fat deposition, and migration. Existence energy varies inversely with environmental temperature. Food intake, the sole source of existence energy as well as productive energy, decreases directly with photoperiod. Migration, in some species, allows the avoidance of a winter photoperiod which is too short to permit a food intake adequate to supply the minimum existence energy. From the standpoint of migration, the results of these investigations are significant in at least two ways. (1) They demonstrate an important basis for selection in the evolution and maintenance of migratory patterns. (2) It is possible that changes in physiologic condition associated with energy intake and the available productive energy (see also Merkel, 1938, and Putzig, 1939) in response to annual environmental cycles may initiate, in some species, the stimulus which results in migratory behavior. I believe that the philosophies of Kendeigh, Wolfson, and the European investigators such as Merkel, Putzig, and Groebbels are not as divergent as the first examination of their papers might lead one to think. In general terms, the energy relationships and utilizations demonstrated and discussed by Kendeigh may be effected by the endocrine functions emphasized in other theories.

The rhythmic reappearance of the apparently characteristic metabolic condition necessary for, and concurrent with, migration has naturally led to reflection concerning a fundamental regulatory organ with an intrinsic rhythmicity or which responds to a

rhythmic physical cycle of proper frequency. The previously discussed hypotheses involving the gonads and the thyroid gland are attempts in this direction. The inadequacies of these hypotheses has been indicated previously. Among the obvious possibilities of such a fundamental regulatory organ is the anterior lobe of the pituitary gland. This has been suggested by Bissonnette (1937), Putzig (1938*b*, 1938*c*, 1939*a*), and Wolfson (1942, 1945); only Wolfson has presented actual evidence and this is somewhat fragmentary. Rowan (1946) and Bullough (1945) deny such a role by the pituitary gland. The frequent, though not necessarily close, correlation between migration and certain phases of the reproductive cycle make probable a role of the anterior lobe of the pituitary in relation to both. If this assumption is true, it is then possible that the relatively large body of information concerning pituitary-gonad relationships may be useful in interpreting the role of the pituitary in the physiology of migration. Much of this information has been summarized by Bissonnette (1937) and Witschi (1935). Benoit (1935, 1937), Marshall (1936), and Wolfson (1941) have suggested, with some evidence, that the anterior lobe of the pituitary reacts to changes in light via the hypothalamus. Wolfson has placed emphasis on "wakefulness" in relation to the role of the hypothalamus. Consideration should be given also to the results presented by Ivanova (1935) from lighting experiments with English Sparrows from which she concluded that the pituitary gland may be stimulated simply by exposure of the general body surface to increased light. It would seem that these experiments should be repeated.

It should be pointed out here that photoperiodism, that is, periodically increasing or decreasing day lengths, has been suggested, by one mechanism or another, as basic to migratory behavior in the writings of many investigators including von Homeyer (1881), Schäfer (1907), Bretscher (1915), von Lucanus (1923), Eifrig (1924), Rowan (1925, 1926, 1931), Groebels (1928), Wachs (1926), Wetmore (1926), Thomson (1936), Bissonnette (1937), van Oordt (1943), and Wolfson (1942, 1945). That increasing day length could serve as the basis of the physiologic condition necessary for migration has been experimentally demonstrated or strongly suggested by Rowan (1926, 1929) for Slate-colored Juncos by actual departures; by Wolfson (1942, 1945) for migratory races of Oregon Juncos by fat deposition and actual departures; by Putzig (1938*c*) for European Robins, European Redstarts, and Garden Warblers on the basis of recording of *Zugunruhe*; by Schildmacher (1937, 1938*b*) for European Redstarts and European Robins on the basis of *Zugunruhe*; by de Bont (1947) for Chaffinches on the basis of fat deposition; and by Miller (1948) for Golden-crowned Sparrows on the basis of fat deposition.

Although a hypothesis involving a cyclic function of the anterior lobe of the pituitary gland resulting from stimulation because of increased day length and decline in function because of decreased day length is attractive, there can be no general application of it in such a simple form. Few migratory cycles correspond symmetrically to the annual pattern of decreasing and increasing day lengths. Likewise such a simple hypothesis would be untenable for transequatorial migrants and for many types of migrations which occur in the tropics (Moreau, 1931). The first two objections can, in part, be circumvented by the assumption, as suggested by Bissonnette (1937), of the development of a refractory period by the anterior lobe of the pituitary gland (or another endocrine gland or glands), following a period of prolonged activity, whether it is caused by stimulation by an external agent or not. Riley (1936) has shown such a refractory period to exist in the English Sparrow in fall (September) during which time a pituitary-gonad response failed to develop with increased lighting. Wolfson (1945) demonstrated a similar period in immature resident Oregon Juncos in fall. Similarly Miller (1948) demonstrated a refractory period in Golden-crowned Sparrows in fall

during which increased light was ineffective in causing recrudescence of the gonads and deposition of fat. More recently Miller (1949) has been shown that the testes in this species during this refractory period can be stimulated to recrudescence by gonadotropic hormones. This increases the probability that the refractoriness of the pituitary-gonad mechanism lies actually in the pituitary gland.

Although there is ample evidence that some gonadal cycles, and possibly some migratory cycles, are controlled by the pituitary as influenced by photoperiodism and further that refractory periods as suggested by Bissonnette (1937) may be involved, this cannot constitute a completely general explanation for the cyclic regulation of migration. Such a mechanism would not seem feasible as the basis for tropical migratory movements which are correlated with rainy and dry seasons (Moreau, 1931). These should be examined from the standpoint of energy intake and availability and utilization of productive energy. Likewise it has been shown by Witschi (1935) that some gonadal cycles may be the reflection of an inherent internal cycle involving the pituitary gland; possibly the same could be true in some instances for the migratory cycle. Moreau (1931) suggested that there may exist all degrees of variation of migratory cycles from those which are completely dependent on photoperiodism to those with a complete dependence on internal cycles.

Moreau *et al.* (1947) have presented data on the gonadal cycles of the Black-capped Bulbul (*Pycnonothus xanthopygos micrus*), the Yellow-streaked Bulbul (*Phyllastrephus flavostriatus tenuirostris*), and a Mouse-bird (*Colius striatus mombassicus*) in Tanganyika at five degrees south latitude. Moreau is of the opinion that photoperiodism is not a factor since recrudescence occurs when day length is increasing at a rate of only 20 seconds per day. Baker *et al.* (1940) found recrudescence of the gonads of the Golden Whistler (*Pachycephala pectoralis*) in the New Hebrides to occur when day length was decreasing. Admittedly these data on gonadal cycles do not have a direct relation to migratory cycles. Nevertheless they indicate further the possibility of pituitary cycles not primarily associated with photoperiodism.

It is not within the province of this paper to cite and discuss the almost innumerable papers which are concerned with the role of meteorologic and other external environmental factors, such as decrease or change in food supply, in the initiation of migration although this aspect of the problem must enter into the construction of a general working hypothesis of the annual stimulation of migration. The possible roles of these factors, both as initiating and modifying influences, have been discussed at length by, among others, von Homeyer (1881), Cooke (1913), Wachs (1926), Groebbels (1932), Kendeigh (1934), Lincoln (1935), Nice (1937), Thomson (1942), von Haartman and Bergman (1943), and van Oordt (1943). Of particular interest are the suggestions that a bird in *Zugdisposition* is actually stimulated to migrate by an external stimulus, such as a change in temperature, which is effective in the stimulation of migration only when the bird is in *Zugdisposition*. This idea was discussed in principle by Wachs (1926) and suggested more positively by Groebbels (1932). Palmgren (1936) suggested that a drop in temperature may be the stimulus for fall migration in Goldcrests (*Regulus regulus regulus*). Putzig (1938a, 1939a) has presented evidence to support a similar contention for the European Robin. He also (1937, 1938a) noted increased *Zugunruhe* in spring in European Robins with increased temperatures. These observations have been confirmed by Schildmacher (1938a) for the same species. Merkel (1938) has suggested that Whitethroats and European Robins in *Zugdisposition* in fall may be stimulated to migrate by external factors such as a drop in temperature which he believed to be effective through increased thyroid activity. Actually, however, such observations

do not necessarily indicate whether migration would or would not have occurred in the absence of the external stimulus.

Van Oordt (1943) in reviewing the physiology of migration has suggested that migratory birds come into *Zugdisposition* as the result of internal physiologic rhythm and that during, and only during, the period of *Zugdisposition* can external factors be operative in stimulating migration. Vleugel (1948), on the basis of his observations of the winter movements of certain species of waterfowl and shorebirds in the Netherlands, has suggested that certain species, or populations thereof, may be in *Zugdisposition* throughout the winter. This would constitute a basis for winter movements in response to meteorologic changes. This suggestion, although hypothetical, is important and should be subjected to experimental investigations.

Migration is the result of the release of a complex inherited behavior pattern stereotyped in the nervous and endocrine systems. Presumably such patterns have evolved by variation and selection as in the evolution of morphologic features. Among the selecting factors may be more favorable reproductive conditions in summer in the breeding area, more favorable energy intake and energy relationships in winter (as suggested by Kendeigh), unfavorable summer temperatures in the winter area (Kendeigh, 1934), and more favorable nutritional conditions. Much more attention should be given to this aspect of migration. Complexities may conceivably exist because of temporal changes in selective factors and the retention of patterns which no longer have positive selective value but which likewise do not have significantly negative values.

Finally it should be pointed out that whatever may be the physiologic changes involved in the stimulation of migration, they must in some way affect the nervous system so that the migratory behavior pattern may be released. This problem has been recognized and discussed, among others, by Wachs (1926), Kendeigh (1934), and Palmgren (1944b).

#### A WORKING HYPOTHESIS

In devising this hypothesis I have had in mind constantly the possibility that migration may be, and most probably is, a phenomenon of multiple origin. It is consequently mandatory that a single hypothesis be constructed in only the most general terms. Further, this hypothesis is constructed with full realization of the extremely fragmentary nature of our knowledge, both from experiments and from observations under natural conditions. The ideas in this hypothesis are not original, as the materials presented previously in this paper indicate. I confess that I have no profound faith that our ultimately acceptable theories of the annual stimulation will necessarily retain any substantial part of this simple hypothesis. I do hope that this will serve as an inventory of our present knowledge and as an impetus for further thinking and planning of investigations.

It is proposed that periodically, twice annually in most species, the migratory bird comes into a distinct metabolic condition, probably as a phase of a fundamental metabolic cycle, which places the bird in a "disposition to migrate" (*Zugdisposition*). This disposition to migrate may be reflected in the deposition of fat characteristic of the beginning of migration of some species and is doubtless associated with changes in energy utilization. Other physiologic aspects of *Zugdisposition* have been mentioned previously. Data are still much too fragmentary to permit comment on possible differences in spring and fall disposition and the mechanism which fixes the direction of migration (Geyr von Schweppenburg, 1938; Merkel, 1938). The fundamental cycle which periodically places the bird in the disposition to migrate is probably the result of a cyclic function of the anterior lobe of the pituitary. This cycle could be the result of periodic change in stimulation by periodic external physical factors, changing photo-

periodism for example; or this arrangement could be modified by refractory periods following the period of stimulation; or the cycle could result from more strictly internally fixed rhythms of the pituitary alone or resulting from the interaction of the pituitary and other glands. The length of the periods of disposition to migrate must be assumed to vary considerably within and among species. Perhaps among "vagrants," "wanderers," and certain winter visitants in temperate areas (Vleugel, 1948), there may be a single period extending from the end of one breeding season until the beginning of the next. The length and actual development of the periods of disposition to migrate may also be a function of age and other factors within the species. It would be expected that the gonadal cycle, in many instances, would show certain correlations with the migratory cycle, since both are presumed to be based on the cyclic regulatory effects of the pituitary. It is not the intent of this hypothesis to exclude gonadal effects and influences from this suggested fundamental metabolic cycle. Rather it is intended to place primary emphasis on the anterior lobe of the pituitary gland in the regulation of this cycle. It is likewise considered as improbable that the gonads are a generally essential part of the immediate stimulatory mechanism.

During the period of disposition to migrate, and only during this period, external stimuli may be effective or necessary in stimulating the actual initiation of migration. For the time being it seems best to assume the greatest possible variation from total lack of necessity to complete necessity of external stimuli for the initiation of migration. It would appear in the cases of many early fall and late spring migrants that external stimuli may be unnecessary and that migration will begin in response to internal stimuli associated with the metabolism of the disposition to migrate (*Zugdisposition*). On the other hand it seems quite evident that in many cases, particularly among early spring and late fall migrants, an external stimulus during the period of migratory disposition is requisite for the initiation of migration. The failure of the occurrence of such stimuli, such as a sufficient drop in temperature, during the period of disposition to migrate, has been suggested as the explanation for the increased occurrence during recent decades of normal migrants in the breeding areas in winter in the northern United States and northern Europe, as described by Siivonen and Kalela (1937) and Lehtonen (1948) among others.

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