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LIGHT VERSUS ACTIVITY IN THE REGULATION OF THE SEXUAL CYCLES OF BIRDS: THE ROLE OF THE HYPOTHALAMUS

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INTRODUCTION

The desire to induce migration of birds experimentally incited Rowan to devise a method whereby he could stimulate the development of the gonads, for he believed that if birds were liberated in the winter period with recrudescent gonads they might migrate north on release. Through artificial illumination from ordinary electric light bulbs, juncos were subjected to increasing day lengths, and in spite of extremely low temperatures the gonads developed, some testes almost reaching maximum size. Consequently Rowan undertook a number of experiments in bird migration. These have been critically examined and discussed elsewhere (Wolfson, 1940). In addition, he performed an experiment to determine whether exercise could replace light as the stimulating factor. From the results he concluded that light was important only in so far as it enabled the birds to exercise, and that the daily increase of activity was the factor which induced gonadial growth.

Since Rowan's initial work there has been much experimentation. The effect of light upon the gonads has been confirmed by the manipulation of the sexual cycles of many species of birds and of other vertebrates. Corroborative data for Rowan's "exercise theory," however, have not appeared. Instead, the work of Benoit, Bissonnette, Riley, and others has led to the conclusion that light itself, qua light, is the real factor involved and not activity.

Although numerous experiments have been performed to determine which theory is correct, the problem is still basically unsolved, and the available data are contradictory and confusing. It is the purpose of this report to attempt an elucidation of the problem by critically examining and discussing the evidence offered in support of each theory and by presenting a new interpretation of the valid evidence.

PRESENT STATUS OF THE PROBLEM

Rowan bases his theory on the results of two experiments and on his investigation of the sexual cycles of London and "country" starlings. The experiments involved the substitution of "compulsory exercise" for the daily increments of illumination. The apparatus consisted of two moving bars which swept all possible perches in the experimental cage every 20 seconds. It was necessary to conduct the experiments in a room with feeble light to enable the experimental birds to see the bars. The first experiment began on March 17 and ended April 28. The number of birds used was small: 6 experimentals, only 4 of which gave valid results, and 3 controls. The results are given below (measurement is average length of the two testes):

Experimentals	Controls
1. Mar. 25 — 1.2 mm.	1. Apr. 3 — 1.0 mm.
2. Apr. 9 — 1.5 mm.	2. Apr. 11 — 1.0 mm.
3. Apr. 12 — 1.6 mm.	3. Apr. 28 — 1.3 mm.
4. Apr. 28 — 3.4 mm.	

Rowan concluded from these results (1929: 202) "that the light increases . . . afford the birds the opportunity of increasing exercise, and that this is the crucial factor in inducing the development of the gonads."

The validity of Rowan's conclusion has been doubted because the gonads had already begun to recrudesce before the experiment was undertaken. Another objection is that the birds were on a 13.5-hour day and had been subjected to normal spring increases of day length before they were placed on a basic 9-hour day at the beginning of the experiment. It is known that such a sudden reduction in day length has an inhibitory effect on the normal gonadial cycle. After four weeks of exercise treatment, when the day length for the experimentals had reached 13 hours, the gonadial growth was slight. Two weeks later, the day length having been maintained constantly at 13 hours, one sample showed a marked development. The testis sizes of all the experimental samples, however, can be found in wild birds on similar dates. This is shown by Rowan's graph of the gonadial cycles of wild juncos (1929, pl. 32), and by data which I have collected. Juncos that were retained at Berkeley showed lengths of testes (average of the two) between 3.3 and 5.7 mm. on April 28. It seems, therefore, that the increased daily activity did not induce gonadial growth, but merely permitted an approximately normal rate of growth to continue in spite of the inhibitory effect of the reduction to a basic 9-hour day length.

Rowan repeated the experiment in 1937 to invalidate the objection that the experiment occurred at too late a date (Rowan, 1937). The technique was similar, but the experiment was begun on January 4 and terminated on February 28. The lighting schedule was altered so that all the birds were on a basic day of 7 hours for the first week, and 8 hours for the remaining seven weeks. The day length of the experimentals on February 28 was 14 hours, 8 hours of normal daylight and 6 of enforced activity. The results are not as striking as in the previous experiment, in spite of the eight weeks of treatment as compared with six previously, but recrudescence, little as it was, occurred in the experimentals, whereas the control showed no response. Only a small number of birds was available, for they were shipped to England where the experiment was performed and there was a high mortality in transit. The number used is not stated, nor are measurements of the testes given, but from the photograph of the testes, it seems that there were three experimentals and one control. The maximum size reached by the experimentals, as calculated from the illustration, did not exceed 1.4 mm. in length.

The original objection of a late start was overcome by beginning this experiment on January 4 when the gonads were at winter minimum, but again the objection arises that the gonadial growth exhibited by the experimentals did not exceed that of wild birds. The testes of wild juncos collected at Berkeley at the end of February show an average length of from 1.0 mm. to 1.5 mm. This argument may seem extraneous if one feels that since the control showed no development, the development in the experimentals was induced by the enforced wakefulness. But it must be remembered that the control was on a basic 8-hour day, a reduction from the normal day lengths of spring, and that any possible recrudescence which would have occurred normally was *actively inhibited* by this short constant day length. The experimentals, although reduced to this short day length, were given daily increments of enforced activity and this treatment may not have activated gonadial development but merely *prevented the inhibition* of the normal gonadial cycle. The inhibitory effect was well demonstrated by the controls. When compared to birds on a light schedule the development was extremely slow. On this point Rowan writes (1938*a*:384): "The augmented rate so characteristic of light stimulated examples at about the 8th week did not materialize. Only a single bird was available on the last day. A conclusive statement cannot be based on one measurement."

I believe that Rowan, in the above two experiments, has given no evidence that substituting enforced wakefulness for light will induce gonadial development. He demon-

strated, however, that juncos placed on a short basic day after December 21 showed little or no gonadial development, and that enforced wakefulness when substituted for light permitted approximately normal gonadial growth in spite of the inhibitory effect of the short basic day on which the birds were placed. To be certain that enforced wakefulness could induce gonadial growth, experiments should be conducted in November and December. The controls would then receive no experimental reductions in day lengths and a response in the gonads of the experimentals could not be explained by the continuation of the normal cycle. The experimental procedure would be the only possible explanation for any recrudescence which occurred.

In a short note published in the addendum to his recent article, Rowan (1938*a*:402) states that English Sparrows "and juncos were subjected to increasing periods of mechanically induced wakefulness *in total darkness* for four weeks, following a preliminary training period of two weeks in a faint and continuously diminishing glow. The sparrows attained virtually full breeding condition while the juncos were highly developed. . . . These determinations rest wholly on the macroscopic evidence." To my knowledge the details of this experiment have not yet been published, and since we do not know when the experiment was conducted or how well it was controlled, it is not expedient to analyze the results critically at this time.

After the completion of these experiments Rowan (1937, 1938*b*) obtained data on the gonadial cycles of starlings in England to support his theory. He observed that London starlings roosting in feeble light, but receiving constant disturbance from traffic, were maintained in a state of wakefulness more or less continuously until the theatre crowds had gone home, sometime after midnight. This situation apparently was a natural experiment in enforced wakefulness. Examination of the gonads of London starlings in contrast to country starlings revealed that the birds in London showed a precocious development of the gonads in early February. They were approximately two months in advance of the country starlings. To explain these observations Rowan writes (1938*b*: 69): "There appear to be three environmental factors . . . that might be instrumental in inducing precocity in London starlings:—(a) Higher temperatures than at country roosts. (b) The additional light provided by the street lamps in whose rays the birds sleep. (c) An increased day length imposed on them by traffic disturbances. Or the effects might be induced by a combination of two or all of these." After examining these three factors he suggests (p. 75) that "the additional period of wakefulness imposed nightly on the London as against country starlings must be looked upon as the crucial element in inducing premature development of the gonads during the winter months." In this same publication Rowan considers the possibility that the observed differences might be due to racial factors (p. 68):

> The early residents of August and September appear to be certainly natives. Starlings from abroad, chiefly from the shores of the Baltic and the German Ocean reach England in October and November, as has been shown by ringing, while birds ringed in England in winter have frequently been recovered from breeding grounds abroad in summer.... The point of possible importance is whether the foreigners wintering in England are normally in a different stage of sexual development in mid-February from British-bred birds; and if the London birds are all natives and the country residents all foreigners (or vice versa), could such a distinction account for the observed differences?
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> It seems to me that the answer is certainly in the negative. Bissonnette's investigations have shown that this species responds so easily and quickly to the conditioning of the gonads under experimental manipulation that it seems wholly improbable that foreign and native birds, living under the identical weather and food and daylight conditions of England, could vary to such an extent in their sexual development. They are not even subspecifically separable, and cannot be distinguished from each other in the hand.

As improbable as it may seem, it is now an established fact that migrants and residents of the same species of bird wintering in the same locality do show different sexual

cycles, those of the residents being approximatley two months ahead of the migrants, as was observed in the starling. This has been shown for the Oregon Junco (*Junco oreganus*) by Wolfson (1940) and for the White-crowned Sparrow (*Zonotrichia leucophrys*) by Blanchard (MS). With the knowledge that such a condition exists in these birds, Rowan probably would agree that racial differences can explain the differing gonadial cycles of starlings wintering in Britain. Many resident and migrant individuals of the Oregon Junco and White-crowned Sparrow cannot be distinguished in the hand, but after careful study and comparison with series of skins, they can be separated in most instances. A careful study of European starlings would probably reveal the existence of external differences in resident and migrant populations. If these populations have existed separately for a great length of time, and if no large amount of hybridization has occurred, morphological differences should be in evidence today.

The recent work of Bullough and Carrick (1939) seems to leave no doubt, at least not in my mind, that there are two races of wintering starlings in England, one resident and one migratory, the former with an earlier breeding cycle. Resident starlings collected between March 11 and March 21 from a quiet residential district two miles from the center of Leeds, where they were roosting under eaves and where there was no increase in numbers in winter after the migrants arrived, had testes that were mature with the seminal vesicles containing spermatozoa. These birds were not subjected to traffic disturbances, yet their gonads were equivalent to those of London Starlings. Starlings were also obtained between March 7 and March 14 from a roost which had been established in the previous autumn. These birds were mostly of continental origin and similar to Rowan's country starlings. In 15 males the testes were small and dark gray in color. One male, however, was entirely different. The testes were almost fully mature. Although obtained in the country, this bird was in the same condition as those collected near Leeds. It appeared therefore that a number of resident starlings were present among the thousands of migrants occupying the roost. This was confirmed when all the continental birds left on March 15 and a population of about 1000 starlings remained. Between March 22 and March 25 seven males collected from this population showed testes similar to those of the male collected on March 9. These birds were clearly local and it was determined that they came from a small area of some five square miles immediately adjacent to the roost.

Rowan should have collected resident birds from a locality where they were not disturbed at night. All of his country samples unfortunately were migrants.

It is to be regretted that Bullough and Carrick do not mention the fat condition of the migrants collected between March 7 and March 14. The migrants left the roost on March 15, and according to our studies at Berkeley, migratory individuals show a heavy fat deposition prior to departure. The residents show no such fat deposition in the spring.

This new information about starlings should be of great interest to American ornithologists, for the starlings introduced on this continent have shown definite signs of splitting into resident and migratory populations. It would be valuable to collect a series of gonads from two such different populations to determine whether comparable differences can be found.

Because of the defects of Rowan's experiments and because it has been conclusively shown that the sexual precocity of London starlings is not due to wakefulness but to racial characters, it is clear that Rowan's activity theory is at present not well supported.

Bissonnette (1931) repeated Rowan's activity experiment, but was unable to corroborate his results. Upon study of his technique, however, I feel that the experiments are not comparable, and that it can reasonably be questioned if Bissonnette's "work" experiments demonstrated that increasing periods of wakefulness in birds cannot be a factor in inducing gonadial development. Bissonnette used the starling for his experi-

ments, and the individuals, according to him, were residents. The juncos used by Rowan were migrants. This is an important distinction, for Wolfson (*loc. cit.*) and Blanchard (*loc. cit.*) have shown that resident and migratory races of the same species differ distinctly in their physiological response to identical environmental conditions. Even disregarding this fact, other objections can be raised to Bissonnette's work. The irregularity of the daily increment of muscular exercise was marked. The belt in the "work" cage caught for short periods and its release was delayed on many occasions. "Times from three hours onward were variable as shown by the graph . . . but there was a general increase in time of experimental treatment up to between six and seven and a half hours per night and none thereafter, with the exceptions due to accidents and shown in the graph" (p. 288). He argues that "these vagaries are not believed to be very significant because the amounts of light to which birds are subject in nature vary from day to day as a result of atmospheric conditions," but it is not probable that they would experience the differences to which they were subjected in this experiment. It is most certainly true that they would not show the abnormal behavior of the birds in the work cage. Of their behavior Bissonnette writes (p. 288):

> It was soon noted that the birds in the "work" cage, instead of trying to remain on the roost to be forced off by the cross-strip on its circuits, after one or two experiences with the strip, flew up and hung braced by their tails and claws from the wires of the sides and the end of the cage nearest the light, and only occasionally, when fatigued, sought rest on the roost, to be started off again in less than twenty seconds. They did learn to step over it a few times when tired, but seemed to prefer to hang from the wire most of the time when the machine was going. When it stopped, they soon came to rest on the roost. In none of the cages did they roost on the floor. Birds in the "light" and "inside control" cages did not behave in this way.

Can one rely on the results of such experiments when the behavior of the subjects is so abnormal? Bissonnette dismisses the behavior of the birds as being of any significance by stating (p. 289):

> That the enforced work did not interfere with the general health of the birds subjected to it is shown by the fact that during the whole experiment from December 4th to May 11th only one bird was found dead in that cage, and he had been caught by the cross-strip at one end of the roost and wedged in against the end of the cage, at the place of exit of the belts, and killed by constant pressure on his body. The fact that he did not fall to the floor of the cage is evident [sic] he did not die from disease or starvation, but was caught and held.

Must a factor in an experiment cause the death of the subject before it can be considered important in altering the results?

Even if one dismisses the objections raised above, as Bissonnette does, and considers his results valid, there is still reasonable doubt about his conclusion that light *per se*, and not wakefulness, is the factor which induces gonadial development. Bissonnette's experiments were conducted from December 4 to May 11 and, with the exception of one male, all males were worked during a period when the gonads were recrudescing. In addition, all birds were subjected to normal day lengths until March 19 when the day length was 12 hours. From March 19 to May 11 a constant day length of 10 hours was maintained by shuttering the room from 5 p.m. to 7 a.m. Because of these lighting conditions and because the gonads had already begun to recrudesce, it is impossible to determine from these experiments whether or not daily increases in the periods of wakefulness can induce gonadial growth. Is Bissonnette justified, therefore, in concluding that added exercise periods without light are not effective in inducing gonadial activity in the starling?

The enforced wakefulness, as in Rowan's experiments, did modify gonadial activity. On March 19 two newly captured starlings with enlarged gonads, one male and one female, were placed in the work cage. They received 10 hours of daylight, a reduction of two hours from normal day length, plus 6 to 6½ hours of work each day until April 15

when they were autopsied. The gonads of the worked birds were larger than those of the "inside controls" whose "light history" had been the same and whose gonads had undergone some regression as a result of the reduction to a constant 10-hour day length. Bissonnette concluded (1931:298) that "they had either continued to increase in size and activity after the 'inside controls' started to regress, or else had been slower than they in regression. In either case they lag behind the inside controls as a result of more daily exercise." This signifies that the exercise prevented gonadial regression.

Two birds that were worked from January 15 to April 15 had testes that were "medium" and "enlarged considerably" (p. 290) and were not greatly different from those of birds worked only from March 19 to April 15. The testes of the control were small as a result of regression. These results lead me to the conclusion that enforced exercise, or wakefulness, permitted a subnormal rate of gonadial growth and prevented regression in spite of the reduction in day length.

The differing gonadial cycles of migrant and resident starlings may prove to be of great significance in future work with starlings in this country. Although a species may be "resident" in a locality, the individuals may be migratory. Whether this has been a complicating factor in Bissonnette's experiments is difficult to say. Future work on this point is certainly necessary.

Riley (1940) has performed experiments somewhat similar to those of Rowan and Bissonnette in that a mechanical activator was employed. Riley's induced activity, however, occurred in complete darkness in a revolving drum. The subject was the English Sparrow, and the individuals were probably residents. His results showed that activity in complete darkness did not affect the gonads, but that if light was present in the activity chamber the gonadial response was similar to that of birds on a lighting schedule alone. He concludes that there is little doubt about the importance of light itself in regulating the sexual activity of the sparrow. He thinks that the positive results obtained by Rowan in his activity experiment may be explained by the fact that light and activity were not completely separated. The experimental birds which were awake could perceive the feeble light, while the controls which were asleep "with closed eyelids and heads tucked under their back feathers were subject to none of this additional lighting" (p. 82). Although Bissonnette's activity experiments were conducted in feeble light, some of his birds failed to show any appreciable gonadial response. Riley (p. 88) explains this by suggesting that "starlings may require higher intensities of light than the junco, or as already suggested by Rowan, negative reactions may be the result of unfavorable excitation of the birds."

In connection with Riley's work a significant objection arises. His birds were not trained in the activating mechanism during the day, as were Rowan's juncos. This point was not stressed by Rowan, or other authors who have reviewed his work.

The juncos were trained in the apparatus during the day apparently for some time before the start of the experiment. In his original report on the experiment (Rowan, 1928:11) he remarks: "After the birds were deemed to have got accustomed to the device a second transverse bar was attached at the opposite point of the belt. As they soon developed a system of merely hopping over it, the exercise could scarcely be described as strenuous." He implies that they were trained in the daytime, because at the onset of the experiment both bars were apparently on the belt. No explicit statement of this matter is made, however, until a later publication (Rowan, 1931:125).

This factor, I believe, is of the utmost importance, for if the state of wakefulness of the birds is conditioned to the stimulus provided by the apparatus, then one can be reasonably sure that the experimentally added wakefulness is definitely linked to the nervous system. It is difficult to believe that birds revolved in small cages within a dark chamber, in which they had not been before in the light, could undergo a normal state

of wakefulness. Riley himself remarks (p. 83): "In the revolving activator lighted, it could be observed that some of the birds were more excited than is customary in light experiments." If they were abnormally excited in the light when they could see where to move as the drum rotated, it is difficult to believe that they were not more excited in the dark as their bodies were forced to move. There is no doubt that the birds were not asleep, but I think it is questionable whether they underwent a normal state of wakefulness in the activator.

The above experiments in birds are the only ones to my knowledge that have attempted directly to substitute wakefulness for light as a means of activating the gonads. In each case it has been shown that no conclusive evidence has been presented to prove that light itself is the stimulating factor, or that wakefulness is the stimulating factor. Other types of experiments, however, have been done which have yielded important information relative to the problem.

The experiments of Benoit on ducks (1937) have shown that light cannot affect the gonads in hypophysectomized birds. *A priori* one would expect this to be true, for the anterior lobe of the pituitary produces the gonadotropic hormones, and without these the gonads cannot develop. Realizing the indispensability of the pituitary in the light reaction, most authors think that the light stimulates the pituitary to secrete the gonadotropic hormones which in turn stimulate gonadial development. That this is true cannot be doubted, but the original problem still remains. The pituitary is essential, but by what means does the light affect the pituitary?

Rowan naturally believes that the stimulus is the state of wakefulness, but he offers no precise explanation of how the state of wakefulness can induce the gonadotropic activity of the pituitary. This weakens his theory considerably. He writes (1938*b*:73): "Little seems to be known of the physiological changes induced by altering the relation of waking to sleeping hours, yet .... the accumulated experimental evidence as it now stands, in spite of many apparent contradictions, does not preclude the possibility that it is such changes—little as we know about them—that are primarily instrumental in the activation of the pituitary and gonads." His argument is certainly valid, and, as will be shown later, it probably has not received an accurate evaluation.

Benoit, Bissonnette, and others adopt the view that the light affects the anterior lobe of the pituitary through a receptor and that light itself is the important factor. The receptor immediately investigated was the eye, and the results of various investigations have been inconclusive. Other receptors have been suggested such as the skin, and the region of the head around the eye, but again, even considering the quantity of the work which has been done, especially by Benoit, the results have not led to explicit and decisive conclusions.

DISCUSSION AND CONCLUSIONS

After a careful study of both sides of the problem, and the recent work in related fields, it seems to me that there is an explanation which could embrace both the light and activity theories and nullify the present controversy. This explanation is not based on incontrovertible facts, but in the light of our present knowledge it seems to be more than just a possibility. I think it should be taken into consideration in future experiments, as well as in our search for the factors which regulate the sexual cycles of birds under natural conditions, for in these ways alone can it be tested and its value determined.

When the gonads of birds, whose sexual cycles can be manipulated by light or activity experiments, are recrudescing, whether they are under experimental conditions or under natural conditions, the amount of time spent in activity, or wakefulness, is increasing daily, and conversely, the amount of sleep is decreasing. As a result of the work of Kleitman (1929) there is little doubt among physiologists that the cycle of sleeping and waking is controlled by the central nervous system. Kleitman's well accepted theory of sleep,

briefly stated, is that due to fatigue, habit, etc., the subject will relax its muscles, close its eyes, and in other ways decrease afferent impulses to higher centers; this abolishes motor activity due to increased synaptic resistance in the higher centers so that subthreshold impulses are not critically analyzed. Impulses arising out of primitive processes and reactions such as hunger, thirst, and muscular movement cause awakening, but the ability to keep awake throughout the day is dependent, on the other hand, upon the development of conditioned reflexes. As long as the impulses from the different distance receptors can be analyzed by the cortex the state of wakefulness will be maintained. If the stimuli are not received from the periphery or cannot be analyzed by the cortex the subject is unable to remain awake. The state of wakefulness is, therefore, an acquired phenomenon and not inborn. Infants and very young animals do not show it.

Although Kleitman's work was well received, it remained for Ranson (1939) and Ranson and Magoun (1939) to develop the theory and put it on a neuro-anatomical basis. The problem had been the localization of the areas involved. On the basis of their recent work, it is clear that the hypothalamus plays an important rôle in sleep regulation. A large part of the literature (reviewed by Harrison, 1940) supports the belief that decreased activity of the hypothalamus results in somnolence and that increased activity of the hypothalamus results in bodily activity. The works of Kleitman and Ranson fit well together since, as pointed out by Harrison, it may be assumed that cessation of incoming impulses allows a decreased activity of the hypothalamus with a consequent decrease in its excitation of the brain and body.

Hypothalamic control of sleep alone could not explain the gonadial response of "light treated" birds. It has been shown, however, that the hypothalamus exercises some control over the gonadotropic functions of the pituitary (literature reviewed by Uotila, 1940; Brooks, 1940). It is well known that the anterior lobe of the pituitary produces the gonadotropic hormones. The production or release of these hormones is under the control of the nervous system in some instances, for it is evident that visual, tactile, and behavioristic stimuli can affect the pituitary in birds. In the pigeon, ovulation occurs only after copulation or as a result of emotional excitement; isolated birds do not ovulate. Sight of an incubating female induces in a male pigeon the changes necessary for crop milk secretion. For any species of bird the number of eggs in a clutch is generally constant, and when the proper number is attained, ovulation ceases and incubation begins. The stimulus for the cessation of ovulation may be tactile, or proprioceptive, or visual. After a critical survey of the field, Brooks concludes that there is much to suggest a neural modification of hypophysial gonadotropic functions, but very little conclusive evidence to prove or disprove this theory; in certain species experiments have clearly demonstrated that the hypothalamus influences the gonadotropic activity of the pituitary.

On the strength of this present knowledge of the relation of the hypothalamus to sleep and gonadotropic activity, I propose the following explanation of how increased daily illumination can cause recrudescence of the gonads under experimental and natural conditions. As the days increase in length, birds are awake for longer periods of time because the state of wakefulness, at least in some birds, is a conditioned response to light; the concomitant activity of the hypothalamus causes an increased production or release, or both, of the gonadotropic hormones from the anterior lobe of the pituitary; these, in turn, stimulate gonadial recrudescence. This is by no means the complete picture of what occurs, but it can explain adequately most of the results which have been obtained in light and activity experiments with birds.

The position of the hypothalamus in the above explanation is strengthened by the fact that it is the center for temperature regulation, and it plays a part in fat metabolism. Riley (*loc. cit.*) has shown that coincident with lowered body temperature mitotic divisions of the germ cells of the English Sparrow occurred almost exclusively at night. When compulsory exercise or light was administered at night, the mitoses diminished. A com-

plete reversal of day and night by means of shutters and artificial illumination also reversed the normal rhythm of mitotic activity and of body temperature. Wolfson (*loc. cit.*) has shown that during the early stages of gonadial recrudescence prior to migration a heavy subcutaneous and abdominal deposition of fat occurs.

In Rowan's activity experiments the importance of the training which the birds received in the daylight becomes apparent. The stimulus of jumping over the bar became an additional conditioned stimulus for the state of wakefulness, and that is why Rowan's birds showed some gonadial response. Bissonnette's experiments are difficult to interpret correctly because of the complicating factors which entered into them. In Riley's experiments, I believe the birds failed to show a gonadial response because the state of wakefulness was not conditioned to the stimulus provided by the revolving drum. If the birds had been conditioned to this stimulus during the day I expect the birds might have shown a gonadial response. However, to obtain this response they should not become abnormally excited, and their state of wakefulness and sleep should be approximately normal. Concerning the problem of a light receptor, the necessity of one is obviated if the hypothalamus controls the activity of the pituitary as described. The eye is essential in that under normal circumstances it is the only receptor which enables the state of wakefulness to become conditioned to light.

At this point it is necessary to consider some of the experiments of Benoit (1937), for it is on the basis of his results that the light theory is supported by so many authors. It should be noted that Benoit used domesticated Rouen ducks in his experiments.

Benoit demonstrated at first that if the head was completely hooded, there was no response to the increased illumination. If there was an opening in the hood in the region of the eye, however, there was a response to the light despite the fact that these birds were completely trussed in an opaque black cloth. Benoit concluded that light in the region of the eye induced gonadial development. It may be argued, however, that although the bird was immobile, the eye was stimulated and the state of wakefulness was evoked as a conditioned response to the light. The birds without perforations over the eye were not disturbed, but Benoit gives us no information on their behavior. Since the species is domesticated, it is not improbable that they did go to sleep, for the stimuli which normally maintain wakefulness were lacking. Birds with their backs plucked and exposed to light, but with their heads hooded, showed no response.

To determine the rôle of the eye Benoit performed the following experiment. Control birds, birds with one or two optic nerves sectioned, and birds with both eyes removed were placed in two mixed groups, one in a lighted room and one a dark room. In these groups were birds without hoods, with hoods, and some with hoods plus perforations over the operated eyes. In those cases where the light could strike the orbit, or eye with the optic nerve cut, there was a gonadial response. If the head was hooded there was no response, unless there was a perforation in the hood in the region of the eye. Benoit concluded that the eyes are not necessary for the gonadial response to artificial light. He does not give us any information about the behavior of the birds and it would be difficult to interpret this experiment from the standpoint of wakefulness. This experiment rather suggests that direct illumination of the cut optic nerve, or hypothalamus, or pituitary, or eye with optic nerve cut, can induce gonadial development.

In a similar experiment of Benoit's (1935), where normal birds were in the same pen with birds some of whose optic nerves were sectioned and others whose eyes had been removed, all birds showed a gonadial response. Rowan (1938*a*:382) criticizes this experiment by stating that the normal birds acted as a disturbance for the operated birds and hence induced wakefulness in them. This may be true for this experiment, but in the experiment cited previously, this criticism is invalid, because two normal birds were included in the group in the lighted pen.

Another series of experiments was performed involving direct illumination of the orbit with the eyes removed. In one experiment the orbits were plugged with hemispheres of opaque rubber. Eight birds with both eyes removed were free to move so that they received artificial illumination on their heads from all directions. Two birds with only the right eye removed had their heads solidly fixed on a board. The right orbit received a beam of light directed in such a manner that the region of the optic nerve, hypothalamus, and pituitary were at the center of the shadow cast by the rubber screen. The birds which were free to move and which had rubber cups in their orbits showed a good gonadial response, averaging a little less than the controls without the rubber cups. The birds fixed to the board showed no response. Benoit concluded that the photoreceptor organ which was situated behind the rubber cup was able to receive a little light in the birds which were free to move, but was protected from the light in the birds with their heads fixed to the board. This conclusion is difficult to accept. The controls without rubber cups which were fixed to the board did not show as great a response as the free-moving controls (lacking rubber cups). The response of the fixed controls was even less than in the birds which were free to move and which had rubber cups in the orbits! I think that some details of behavior or other complicating factors are obscuring the correct interpretation. Benoit does not give us any information on the behavior of the birds, nor does he state how and when they were fed. If they were hungry during the illumination they might have been in a state of wakefulness. The results of this experiment make one a little suspicious of the method employed. They suggest strongly that wakefulness may have played a part in the experiment.

That the "fixed birds" with cups showed no response is contradictory to the results of another experiment which was performed on a single bird. Under the eyelids of both eyes were placed lead plates a little larger than the eyeball. The eyelids were then sewn together. The bird was subjected to artificial illumination and it showed a considerable gonadial response. At the autopsy Benoit made a mid-sagittal section of the skull and concluded that the light passed around the metal plate and penetrated deeply, conducted by the tissues, or by diffusion. If the light was able in this instance to pass around the metal plate, why did it not pass around the rubber cup and diffuse through the tissues in the case of the bird whose head was fixed to the board? The behavior of the bird with the lead plates under the eyelids is not described.

In yet another experiment Benoit irradiated the region of the pituitary and hypothalamus directly through a tube of glass. He obtained a strong gonadial response. The illumination was given on two days only out of twenty, a total of about 28 hours being involved. On the basis of what is reported, it is difficult to interpret this experiment in any way but that direct illumination on the pituitary or hypothalamus causes increased production or release, or both, of the gonadotropic hormones. The light acting directly apparently can induce a gonadotropic reaction in the nervous and/or endocrine tissue. However this may be under experimental conditions, under natural conditions I do not think that light penetrates the tissues of the head to stimulate the controlling centers directly. Nor do I believe that a photoreceptor is essential. Peripheral impulses, such as auditory, tactile, and proprioceptive, if they are strong enough can induce wakefulness without the eye, although the eye is without question the most important receptor from the standpoint of stimuli which induce wakefulness.

Ivanova (1935) tried some hooding experiments with English Sparrows. The hood was made of a thin piece of silk and fixed to it in the region of the eyes were pieces of a black opaque material. Her results showed that the hooded birds developed nearly as fast as the unhooded. Benoit's explanation for this positive response is that light leaked around the opaque material. Since her unhooded birds were in the same room and re-

ceived the same illumination there is also the possibility that disturbance of the hooded birds caused wakefulness.

In hooding experiments, Ringoen and Kirschbaum (1937) obtained a positive response in 3 out of 9 birds. Again Benoit questions whether all the light was prevented from passing to the eye. No information is given as to housing or as to the construction of the hood.

From the results of Benoit's experiments it is impossible to conclude that wakefulness is not a complicating factor. Because he does not give the details of the housing and the behavior of the birds during the treatment, one cannot be sure that he has considered wakefulness as a factor. It seems rather that he has overlooked the matter completely. He has demonstrated that light directed at the region of the pituitary and hypothalamus can evoke a gonadial response. This does not indicate as Riley suggests that light, qua light, is the important factor involved and that wakefulness is unimportant. Under experimental conditions light so directed can evoke a response which simulates the response induced by daily increases in wakefulness.

It does not seem probable that daylight increasing 2 to 3 minutes a day under natural conditions penetrates the tissues of the head to stimulate the hypothalamus and pituitary. Light is an important factor in the regulation of the sexual cycle, but only in so far as it provides a stimulus for wakefulness. Since the wakefulness is under the control of the hypothalamus, the hypothalamus becomes the important timing center for the sexual cycle. Similarly, if birds are subjected to a constant short day length in the spring experimentally, the gonads undergo some recrudescence, but there is a great lag behind the normal development. Whether an inherent rhythm of the pituitary, or gonads exists is difficult to say. I think, however, that the lighting schedule which immature birds receive does materially influence their timing system. If this were not true how could one explain the nearly perfect coincidence of migration, or of nesting, in birds hatched one to three months apart?

In all types of environments there is usually a factor (or factors) which is periodic in its occurrence and which is an indicator of the best season for breeding. In the course of evolution this factor has become the regulator for the proper time of breeding through the responses evoked in the nervous system. If this were not true, many species would not have survived until the present day. The sexual cycles of migrants must be particularly well timed, for the breeding season of some species is very short. The hypothalamus, on the basis of recent work, seems to be that part of the nervous system which regulates the time of breeding and of migration. It is the integrator of the impulses concerned with the sexual cycle such as auditory, visual, tactile, and proprioceptive. In some species several of these impulses are important, while in others only one may be important. It has been shown in several instances that the sexual cycles of tropical birds and mammals cannot be manipulated experimentally with light. Yet, there is probably some factor in the environment which influences a timing center in the nervous system. The hypothalamus is probably involved in most species of birds and mammals and perhaps in other groups.

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