

A REVIEW OF EXPERIMENTAL INVESTIGATIONS ON SEASONAL REPRODUCTION IN BIRDS

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MANKIND has known for centuries that domestic hens could be made to lay more eggs in winter by putting lights in the coops at night. Known also have been certain photoperiodic manipulations (Miyazaki, 1934), (Hoos, 1937) through which caged birds could be induced to sing unseasonably. Despite the considerable work which has been done with poultry, the accumulated knowledge concerning photoperiodism in plants, experiments dealing with the effect of light upon plumage (Beebe, 1908), and various theorizings concerning the effect of light upon the annual cycle in animals (Schaefer, 1907, and others), the experimental study of seasonal reproduction has not been attempted until very recently. The work was initiated in 1925, by Rowan, who was interested primarily in migration, and expanded by Bissonnette in 1930.

Rowan's chief finding was that precocious spermatogenesis could be brought about in sexually inactive male Juncos by adding several hours of artificial illumination to natural winter day lengths. Bissonnette, working with the Starling, confirmed Rowan's findings. (For summaries of the avian studies carried on by these two workers, see Rowan, 1938 and Bissonnette, 1937.) The basis for this work was the frequently observed correlation between increase in gonad-size and lengthening of days in spring. This shift in the proportion of daylight-hours to darkness-hours has been known as long as mankind has been aware of the equator, the poles, and the season. The difference between the total of daylight hours on the longest and shortest days of the year is least at the equator and greatest at the poles. Baker (1938b) graphs the day lengths at various seasons and latitudes.

From Rowan's and Bissonnette's observations has arisen the generalization that increase in day lengths induces spring gametogenesis in birds. Much of the work of the past 20 years has tested the validity of this generalization. Rowan himself, on the basis of earlier experiments with the exercising of birds, came to the conclusion that lengthening of days had no direct photic influence upon the gonads, but that it did permit the birds to exercise more. Wolfson (1941) perceived a correlation between degree or incidence of wakefulness and increase in day length and in gonad size. No experiment thus far devised has proven that any external stimulus, *operating in darkness*, induces precocious gametogenesis.

Gonadotropins secreted by the pituitary are believed to stimulate the gonads, release sex hormones, and cause gametogenesis. The release of sex hormones is closely correlated with the development of the reproductive organs, of secondary sexual characters, of some sexually dimorphic characters, and of behavioral

patterns. Reproductive rhythmicity may be, basically, hypophyseal rhythmicity; the activity of the adult gonad merely a reflection of hypophyseal activity. What is it, then, that controls the avian pituitary? The bald answer is that no one knows. What we do know indicates that external environment determines the activity of the pituitary at least to some extent.

We must never lose sight of the fact that the environment of the many species of birds varies widely. What is true of one species may not be at all true of another. We are justified in talking about 'the bird' only when we have learned, through patient observation, that the several species, races, and individuals which we are discussing behave uniformly. Unfortunately, the field naturalist and the laboratory worker often do not understand each other. The one complains that factors operating on the bird in the laboratory are very different from those operating on the bird in a wild state; that results obtained through laboratory observations do not *prove* anything about the wild bird. The laboratory worker, on the other hand, is justified in maintaining that tests, observations, and experiments carried on in the laboratory can and do lead to important and significant discoveries. Environmental factors which may seem of great importance to the field worker may, when tested carefully, prove to be of little significance.

It is unfortunate and regrettable that so little work is being done today in the tropics and the southern hemisphere; and that there is no such thing as a correlated study of trans-equatorial migrants such as might be carried on were the ornithologists of South America, Africa, and Australia organized for collaborating with ornithologists of the northern hemisphere. What little we know—and it is fragmentary knowledge at best—has to do principally with birds of the North Atlantic area and of western North America.

The following review of the literature is not by any means the equivalent of a complete bibliography. I have made a point of discussing at some length the most important papers which have appeared, but unimportant papers I have not even mentioned. With a few exceptions, I have consulted all references while preparing the manuscript. I wish to thank T. H. Bissonnette for the use of his personal library and for his counsel during our association at Trinity College. I wish also to thank E. E. Bailey for his help. My work has been supported largely by grants from the Penrose Fund of the American Philosophical Society.

SEASONAL REPRODUCTION

The studies of Baker (*vide* Baker, 1938b) form an important survey of the seasonal factors that are present throughout the world. Baker's generalizations are sufficiently important to quote verbatim (p. 578):

1. As one goes north from the temperate latitudes one finds a general tendency for the egg-laying seasons of birds of all kinds to start later and later at the rate of some 20 or 30 days per 10° of latitude.

2. As one goes south from the temperate latitudes into the northern tropical and equatorial zones one finds a general tendency for the Accipitres, Coraciiformes, and, to a less extent, the Passeres, to start their egg-laying earlier and earlier.

3. The Charadriiformes, Grallae, Herodiones, and Anseres behave differently. In the northern hemisphere they tend to breed later in the tropical and equatorial zones than in the subtropical and temperate.

4. There is a general tendency for birds in the tropics to reach the height of their main breeding seasons somewhat before the sun passes overhead. Two breeding seasons in the year are therefore quite common, but birds which breed only once select either the northward (Accipitres, etc.) or southward (Grallae, etc.) swing of the sun.

5. The main proximate causes of the breeding seasons of birds in nature are thought to be temperature and length of day in the boreal and temperate zones, and rain and/or intensity of insolation near the equator. The time of arrival from migration is often an important factor.

6. Much egg-laying occurs when days are getting shorter, and indeed it often proceeds rapidly while they are decreasing in length and only between 11 and 12 hours long.

7. There is, however, little egg-laying when the day is shorter than 11 hours, and almost none when it is less than 10.

8. Under natural conditions birds exhibit no tendency to start breeding everywhere when the days reach a certain length nor when they are becoming longer particularly quickly.

Baker (1937) states that not many equatorial birds are known to breed all the year round, despite almost uniform length of day. These generalizations of Baker indicate the need for world-wide testing under controlled conditions. Moreau, Wilk, and Rowan (1947) have studied the testes of 3 species of birds at 5° south of the equator. In all 3 species, the testes were largest between September and March; smallest in the following cooler and rainy season; and became larger when day lengths were increasing by only 20 seconds per day.

Reproduction must first have a genetic basis. While the domestic fowl is in many ways not like wild birds, poultry breeding does demonstrate that reproduction can be modified by genetic factors. Through genetic selection, strains that lay eggs for long periods, that continue to lay despite molt, that have lost broodiness, etc. have been developed. Riddle, Smith, and Benedict (1932) crossed a South American dove, *Zenaidura auriculata vinaceo-rufa*, which breeds the year round in captivity at New York (when protected from cold), with the Mourning Dove, *Zenaidura macroura*, which in captivity breeds only between April and August. The hybrids were intermediate between the parents, i.e. the testes were not reduced in the fall as much as in the *auriculata* parent. Bullough's (1942) studies of the Starling indicate that in Great Britain there are 2 races, a Continental and a British. The Continental race has a longer period of gonadal inactivity; and so-called out of season breeding occurs only in the British race. Among other intra-specific differences might be mentioned the fat deposition (light affected) of resident and migratory forms. This fat deposition does not occur in a non-migrant such as the English Sparrow (Wolfson, 1947). These differences point to the need for considering genetic differences when one compares individuals of a species from different localities.

Attention may be focused too narrowly on the environmental alone. When a group of birds is introduced into a new locality, one should consider the possibility that selection may alter the reproductive pattern.

Baker and Ranson (1938), who have collected a great deal of information on the reproductive rhythms of southern hemisphere birds moved into the northern hemisphere, find that most birds change to the equivalent season. The Australian Black Swan, however, changes from a restricted breeding season to breeding at any time of the year in the northern hemisphere. A few birds (Northern Rosella Parrot, Gouldian Finch, Budgerygah) tend to retain their original southern hemisphere periodicity in the northern hemisphere.

Baker (1938a) has tabulated the egg laying periods for Old World birds. The breeding season of the Starling introduced south of the equator into New Zealand extends from August to December instead of from April to June (as in Britain or Germany). The English Sparrow breeds principally from May to August in Britain, but from August to December in New Zealand. Baker's tables show that the English Sparrow breeds the year round in Ceylon and Great Britain, but not in Germany or subtropical northern India.

A fascinating case is discussed by Davis (1945). Several Silver Gulls (*Larus novae-hollandiae*) were moved from Australia to a zoo in the United States. For 2 years the birds nested in November, following their original custom, then changed to nesting in spring and early summer. After 20 years of captivity, their descendants reverted to a fall and winter breeding. Murphy (see Bissonnette, 1937) found that European Storks confined to Lima, Peru, bred below the equator at the time when they would have bred north of the equator.

A much quoted example is the observation of Witschi (1936) that the Orange Bishop, *Euplectes franciscana*, an African weaver finch, maintained its original timing of the plumage cycle when confined in Iowa. Brown and Rollo (1940) and Rollo and Domm (1943) have shown that this species' plumage cycles and testicular states are modifiable by photoperiodic manipulations. Thirteen to 14 hours with 126 foot-candles of illumination were found to be optimum for the production of nuptial plumage. Thus, an apparently inflexible rhythm proves to be flexible when analyzed experimentally. Friedmann (1937, p. 423) says that two races of *Euplectes franciscana*, found respectively in Ethiopia and the Sudan, have different breeding periods.

Even birds that breed the whole year round, such as the Brown Booby in the Cape Verde Islands (Baker and Ranson, 1938), tend to have 1 or 2 breeding periods in a year. So far as is known, no wild bird has equal reproductive vigor at all seasons; and in no wild species does reproduction occur independently of external influences. The common pigeon breeds almost continuously on farms, but it has smaller gonads in the fall and is depressed reproductively by cold (Riddle 1925, 1938).

The domestic fowl also breeds more or less continuously but it, too, is influenced by the environment. The large literature on the fowl is somewhat obscured by the preoccupation with problems of poultry management. It would be most instructive if the less 'domesticated' breeds were investigated thoroughly. Semen production in the fowl is highest from about November to May and lowest for the rest of the year (Parker and McSpadden, 1942, Wheeler and Andrews, 1943). Jones and Lamoreux (1942) have reported that strains bred for high fecundity mature more rapidly and produce more sperm than do less fecund strains. David (1938) found that injection of androgen induced a seasonal comb growth. (In capons combs may be twice as sensitive to androgen in the winter as in the summer.)

In only a few species of birds is the inherent reproduction rhythm relatively inflexible; and, as has been shown to be the case in *Euplectes*, this inflexibility may not be real. Effect of environment on the labile internal reproductive machinery appears to determine the breeding period for each species. Both the internal cycle and the environment are variables. For example, the Starling on the Atlantic coast breeds about a month later in the Gaspé region (Ball, 1945) than in Hartford, Connecticut or Ohio (Hicks, 1933). This is less than 10° of latitude and fits the generalization of Baker (see above). However, the breeding time in Connecticut and in Great Britain (Bullough, 1942) is roughly the same despite a difference of about 10° of latitude. The climate of Great Britain resembles that of Connecticut more than it does that of the Gaspé peninsula. The sexual cycle of English Sparrows breeding in the United States (Ringo and Kirschbaum, 1937) roughly coincides with that of English Sparrows breeding in Russia, presumably near Leningrad (Polikarpova, 1940), with a difference in latitude of about 20° . Linsdale (1933) found that the peak of the breeding season for birds in Kansas came in June, while at a similar latitude in California it came in April and May. He believed this discrepancy to be correlated with rainy periods and availability of food.

Riddle, Smith, and Benedict (1932) found that the conditions of captivity gave the Mourning Dove a slightly longer than natural breeding period. Rowan (1929) found that the canary, a subtropical bird with protracted breeding season, exhibited pronounced sexual behavior in captivity in winter in Canada. Male canaries which were not lighted at night had larger testes and were more active sexually than captive native Juncos.

EXPERIMENTAL STIMULATION OF GONADS

While the goal of reproduction is the production of viable young, a study of fertile matings may not reveal the factors involved in securing this result. Most of the experimental work has dealt with the male. The female as such, and the reciprocal relationships of the sexes have received little attention. Most

studies, furthermore, have been concerned with the factors inducing gametogenesis. The factors involved in inducing and maintaining the non-breeding condition are less well known.

Tests indicate that all birds that breed seasonally are responsive to photo-periodic manipulations. Scott and Payne (1937) got no response from the guinea fowl. More recently, however, Davis and Penquite (1942) got a slight testicular response (no sperm) through exposing male guineas to continuous light (begun January 31).

The basic test consists in giving sexually quiescent, non-refractory birds a daily period of artificial light added to natural day lengths, or by making an artificial day solely by artificial light. Sperm is produced usually in this way in about 1 month.

Activity and Wakefulness. As a result of his early experiments with the Junco, Rowan (1929, 1938) believed that exercise (and later the general activity resulting from the longer days) acted as the primary stimulus for gonadal activation. Wolfson (1941) modified Rowan's theory to read, "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 gonadal recrudescence." Wolfson reported no original avian work to confirm his speculations.

Bissonnette (1931a, 1937) using Rowan's technique, was unable to confirm Rowan. Riley (1940), and Kendeigh (1941) rotated English Sparrows in drum-like cages in darkness. The daily period of rotation corresponded in length to the usual added period of illumination. No gonadal stimulation resulted from this enforced activity and wakefulness in darkness. Thornton and Cummings (1945) gave (in darkness) an added period of noise as a supplement to short days, and found no gonadal stimulation with the English Sparrow. Benoit (Benoit and Ott, 1944) immobilized ducks, and secured a response to light. Burger, Bissonnette, and Doolittle (1942) kept Starlings awake with flashing light. They could produce stimulation or no stimulation by varying the length of the flashes and the intervals of darkness between the flashes. Strangely enough, the demonstrated fact that, for some species, the blue end of the visible spectrum fails to activate males, has not been mentioned in various arguments. Wolfson (1941) in his long critical paper fails to mention this type of evidence. Starlings subjected to long "days" of blue light act as though they are awake; they feed, bathe, etc. (Burger, 1943). Miyazaki (1934) first noted that captive birds subjected to artificially long days were very quiet and drowsy, though activated sexually.

Whatever the ultimate solution of this problem, the exercise-activity-wakefulness theories, as currently phrased, are clearly inadequate. Thus far, no ex-

ternal environmental stimulus except light has been *shown* to induce complete spermatogenesis in seasonally reproducing birds.

Food. Perry's report (1938) that irradiated food activated English Sparrows sexually was not confirmed by Kirschbaum, Pfeiffer, Van Heuverswyn, and Gardner (1939), or by Perry himself. Bissonnette (1931b) found that Starlings with low protein diet did not respond sexually even when the days were long. Kendeigh (1941) noticed no difference in testicular stimulation in English Sparrows if food was given in restricted periods or over the whole light-period. Birds ate as much food in the first instance as in the latter, but in less time. The relation of food to natural reproduction is not easy to determine. Kendeigh (1941) wrote, "The energy demands for full development of the testes and partial development of the ovaries appear not to be large. . . . The final and complete formation and laying of eggs, however, requires considerable energy output". This is well recognized in poultry.

Temperature. External temperature has no *prohibitive* effect in most birds tested. Rowan's original work was done at subzero temperatures. Bissonnette and Csech (1937) induced pheasants to lay eggs in a snow bank. Kendeigh (1941) compared temperatures of 72° F. with 36° F. for effect on the English Sparrow, and noticed no difference in response. Outdoor weather in Kansas did not depress the breeding of turkeys (Scott and Payne, 1937). Schildmacher (1938) secured testicular activation with *Phoenicurus* at temperatures around 0° F. Suomalainen (1937) found no difference in response to light between one lot of *Parus major* kept at an average temperature of 1.9° C. and another kept at an average of 20° C.

Reproduction in pigeons is depressed by cold (Riddle, 1925). Kendeigh (1941) found that clutch size and egg size of the House Wren were correlated with temperature. A temperature of 67°F. was correlated with more and larger eggs than one of 77°F. Lee, Robinson, Yeates, and Scott (1945) reported that high temperature reduced egg laying among domestic hens in Australia to about once a week. Many eggs were soft and deformed. Some increase occurred even though the heat was maintained. There was found also a difference among breeds in susceptibility to heat. Laying was not abolished entirely. One must distinguish, however, between effects on seasonal reproduction as a whole, and effects on individual ovulations and clutch formation. In the latter 2 examples, clutch formation, rather than the ability to breed at all are influenced. In nature, the ornithologist mostly sees clutch formation or its lack, but does not know more about the ovary.

Burger (1948) found that Starlings kept under conditions of long days and relatively constant temperatures of 90° to 100° F. had testes far larger than those developed in the same time by birds kept under cooler fluctuating temperatures. These warm temperatures, however, did not induce progressive spermatogenesis under short days. The significance of these results is not clear. These

temperatures are higher than those experienced by the Starling for any great time during the normal breeding season. The results do demonstrate that external temperatures approaching the Starling's body temperature do not suppress spermatogenesis nor cause testicular involution.

At Hartford, Connecticut, the winter of 1947-8 was much more severe than that of 1948-9. In early spring of 1948, testicular enlargement occurred in wild Starlings despite the presence of snow on the ground for the preceding 3 weeks and a mean daily temperature of about 30° F. In the milder 1949, testes secured on the same date as those of 1948 were only slightly larger. It is highly desirable that a study be made over a period of several years at different latitudes or for different conditions for a given species, in which both testes and ovaries are studied at different periods in the cycle. Records of nesting times alone do not tell whether the whole breeding complex is delayed, say by cold weather, or whether only a phase is delayed.

Photoreception. The conventional view is that light is received by the eye which sets off an unknown sequence of events terminating in stimulation of the pituitary. It now appears that stimulation of the pituitary is not effected by nerve fibers going to the anterior lobe via the stalk. Drager (1945) found in the chick no fibers from the stalk going to the anterior lobe. Bissonnette and collaborators (unpublished) have cut the pituitary-stalk of ferrets (a mammal) without loss of sexual activation induced by long days. Many data of this type show that the hypothalamus is involved in mammals.

Considerable evidence indicates that the eye is the primary receptor. For example, hooding the head prevented light from effecting stimulation in 6 of 9 English Sparrows (Ringo and Kirschbaum, 1939). The 3 that showed response were assumed not to have had tight hoods. Hooded immature ducks did not respond to light until an opening was made in the hoods (Benoit and Ott, 1944). Ivanova (1935) got in the English Sparrow no suppression of spermatogenesis by hoods; she considers the plucked skin (Ivanova, 1935) as a possible receptor for light. Benoit got no response by illuminating the plucked skin, while Ringo and Kirschbaum (1939) do not confirm Ivanova's hooding experiment.

Benoit (see Benoit and Ott, 1944 for a summary and bibliography) achieved spectacular results in a long series of experiments on immature ducks. He found that light induced spermatogenesis when: 1) the optic nerve was cut but the eyeball remained in the socket; 2) the eyeball was removed and the orbit illuminated; 3) the hypophysis was illuminated directly by a narrow beam of light; and 4) parts of the rhinencephalon and hypothalamus were illuminated by a narrow beam of light. Gonadal response was slight when blue light was used and the eye kept intact, but when the eye was removed and the hypophysis was illuminated directly with blue light, marked gonadal response occurred. Benoit considered the hypophysis to be stimulated by a dual system: 1) an

oculo-hypophyseal system, and 2) an encephalo-hypophyseal system. He believed that both systems are able to function at the same time, i.e. light could stimulate the eye proper and, by penetration of the head, stimulate deeper areas. By illuminating with strong light, half a duck's head, placed on photographic paper, Benoit found that light could penetrate to the pituitary. The penetration was best with red rays, the rays that in the normal duck are the best activators of spermatogenesis. The different effects on the intact bird of various wave lengths of light (see below) would be explained as due to a differential absorption by the tissues of the various wave lengths. Photostimulation is not considered entirely dependent on color vision.

Wave length. Bissonnette (1932a) and Burger (1943) using Starlings, Scott and Payne (1937) using turkeys, Benoit and Ott (1938, 1944) using ducks, find that the blue end of the spectrum stimulates the gonads little if at all. Benoit and Ott (1944), and Burger (1943) agree that the far-red and near infrared are not stimulatory. The most effective wave lengths lie in the yellow-red. Burger (1943) places the wave lengths that will induce sperm in the Starling, approximately between 0.58 and 0.68 microns. There is no evidence that ultra-violet is stimulating or necessary. All investigators, except Rowan (1938) find different effects by different wave lengths within the visible (human) spectrum. Details of Rowan's experiments do not seem to be published.

Light Intensity. The influence of light intensity has been investigated. Burger (1939b) found that when Starlings were subjected to a constant 10.5 hour artificial day, a gradual increase in intensity from Mazda lamps from 25 watts to 500 watts produced no spermatogenesis. Intensity of illumination did not substitute for adequately long lengths of day. Bissonnette (1931b *et. seq.*) first tested intensity in a coherent manner. With long days, Mazda lamps were effective on Starlings in the following order of wattage: $10 < 15 < 25 \leq 40 = 50 = 60$. When a sunlamp was equated with a 200 watt Mazda lamp for luminous intensity, and a 1000 watt lamp equated with the 200 watt lamp for heat intensity, the 200 watt lamp was the more effective. Bissonnette (1932a) found that 1.7 foot-candles of filtered red light was sufficient to induce complete spermatogenesis. The minimum intensity has not been established, but an unmeasured faint light did not stimulate spermatogenesis. On figures given for the domestic fowl (Dobie, Carver, Roberts, 1946) no difference in egg production was found with intensities between 1 and 31 foot-candles.

One rather obvious fact about comparative measurements of intensity seems to be not clearly recognized. Since one may secure a differential effect because of wave length, and since spectral distributions vary with different lamps and intensities, comparative data can only be accurate if monochromatic bands are used. Furthermore, no one has tested the possible significance of a source of light from a single bright source such as a Mazda lamp in comparison with a light that is diffuse.

Bartholomew (1949) working with English Sparrows found that in the fall, 10 foot-candles are less effective than 200 foot-candles from "Daylight Fluorescent Lamp". In the winter however, 10 foot-candles were as effective as higher intensities. Ten foot-candles were more effective than lower intensities. A low intensity of 0.7 f.c. induced sperm in 46 days, while a still lower intensity, 0.04 f.c. was only one-tenth as effective as 0.7 f.c. Relatively low and moderate intensities seemed sufficient to induce complete spermatogenesis, but the rate of response, increased with an increase in intensity. Very faint light, did not, however, induce spermatogenesis, and high intensities were not increasingly effective. One might expect an increase in effectiveness with high intensities due to an increased cranial penetration, if Benoit's theory holds.

Length of Day. Since both intensity of light and wave length vary, and since natural days vary not only in length but also in intensity of light and wave length, experimental work of a quantitative nature should be done under standard conditions. These conditions have not been defined. Each worker has made his own conditions, so most quantitative data in the literature are really qualitative.

Burger (1940) concluded that the minimum day length required by the Starling for the *rapid* production of sperm was slightly less than 12.5 hours. Days of 10.5 hours induced spermatogonial multiplication only. Rollo and Domm (1943) found 13-14 hours optimal for inducing nuptial plumage in the weaver finch, *Euplectes fusciscana*. With poultry, the usual long day administered is 13-14 hours. Bartholomew (1949) secured some interesting data on the English Sparrow. Judging by rate of activation, he found that winter days of 12 and 14 hours were as effective as days of 16 and 24 hours. With days only 10 hours long he was able to secure sperm in 46 days in his 2 experimental sparrows. These 2 birds had previously served as controls for another experiment where they were on days of 8 hours. In another of his experiments (p. 444) one of 2 controls kept on an 8-hour day had a marked testicular development. It might be profitable to repeat these studies on a larger scale. There seems to be a difference between the English Sparrow and the Starling, since in the Starling 10.5 hours of light caused no progressive activity between Jan. 27 and April 20.

It must be noted again, as has been said by many authors, that as one goes toward the equator, day lengths become less and less variable between the solstices. As Bartholomew (1949) pointed out, day lengths even in the United States may remain longer than necessary to activate the English Sparrow. One phase of this problem may have been clarified by work on the Starling (Burger 1939a, 1939b, 1940). Here spermatogenesis did not occur when day lengths were gradually increased from 6 to 9 hours. Spermatogenesis, however, did occur at no reduced rate when day lengths were gradually reduced from 20.5 hours to 16 hours. It was concluded that spermatogenesis in the Starling is

not induced by an increase or a decrease in day length as such, but because the length of day is reached which is sufficiently long to be stimulating.

TESTICULAR INACTIVITY AND REFRACTORINESS

Most experimental work has dealt with stimulation of the testes. In order to secure stimulation the testes must at first be in an inactive state. Such inactive gonads are found in immature birds and in adult birds in what Polikarpova (1940) quaintly calls the "dead sexual season", i.e. the period of testicular quiescence following a breeding period. The quiescent period of the immature and that of the adult are not entirely homogeneous either when compared to each other and when compared to themselves over a period of months. With the immature bird, one must consider the special problem of maturation. Riley (1936) found that additional light given to adult English Sparrows on September 30, induced no subsequent spermatogenesis. Juveniles, however, did respond. Adults lighted on November 18 did produce sperm. Obviously, between September 30 and November 18, the adults passed from a refractory state to a state where light stimulation was effective. Schildmacher (1938) reported that juvenile *Phoenicurus* became completely stimulated by added light only after October 10, but before October 25. Bissonnette and Csech (1938) present an interesting example of the relation of juvenile maturation and day lengths. Ring-neck Pheasants hatched on Christmas day from eggs precociously secured by photoperiodic manipulations, laid 2 infertile eggs on July 25-26 under natural light conditions. These eggs were laid later than the normal season for adults, in the juveniles' first 7 months of life. Here obviously, maturation had progressed sufficiently for the long days of July to be an effective stimulus. Riddle (1931) found that pigeons and ring-doves mature more slowly when the time of maturity as set by the date of hatching, occurs in the autumn. Maturity is hastened in the period February to July. Chicks of the domestic fowl hatched in summer grow more slowly than chicks hatched in winter, presumably because of a reduced feed consumption during hot weather. Night lighting of chicks improved the rate of growth in the summer (Heywang, 1944) in Arizona.

While adult birds can be activated precociously by long days, this stimulus is unable to keep the testes in a continuous state of spermatogenesis. The gonads involute after an active period, just as they do in nature. The post-breeding involution and sexual quiescence is due not to the absence of an initially effective stimulus. In nature, day lengths are still increasing when the gonads of Starlings involute. An internal refractory state develops, i.e. the bird no longer will remain in or initiate gametogenesis when given long days. This refractoriness must 'wear off' before external stimuli can induce a new gonadal activation. The duration of the refractory period in conjunction with the annual light cycle seems to control the *general* form of the annual reproductive cycle of many birds tested. The refractory state may wear off before day

engths are too short to be completely non-stimulatory. Hiatt and Fisher (1947) found that the Ring-necked Pheasant has a partial sexual activation in the fall (Montana). Witschi (1935) writes, "prolonged Indian summers with sunny days extending until late November bring about precocious development of the testes in free living English Sparrows of Iowa". In general, the refractory period lasts so long that autumn days are too short to induce a complete gametogenesis.

This problem of refractoriness is perhaps the greatest relatively unsolved problem in reproduction. A seeming contradiction to the statements about the importance of the refractory state arises from the fact that many investigators have been able to produce 2 or 3 cycles of spermatogenesis in a year. Rowan (1929) first produced for the Slate Colored Junco, 2 spermatogeneses, one in January and the other in May. Miyazaki (1934) secured 2 cycles with Mejiro (*Zosterops palpebrosa*). Damste (1947) induced 3 cycles in the Greenfinch. Burger (1947) got 2 cycles with the Starling.

Results with the Starling (Burger 1947, Bissonnette, unpublished) seem to resolve this contradiction. In all the above cases, the first additional spermatogenesis was produced by first reducing the day length while an active spermatogenesis was occurring and then later increasing the day length. In the Starling, if day length was reduced just as sperm was being first formed due to long day stimulation, the testes promptly involuted. A second addition of long days induced a new spermatogenesis in all birds. If, however, the first spermatogenesis was allowed to continue until a natural involution set in, then a period of short days followed by another period of long days resulted in a less successful reactivation. If a complete involution, produced naturally, was allowed to develop, then a rest of a month on short days followed again by long days resulted in still less testicular activation. In all cases, however, a period of short days was followed by at least some testicular reactivation when long days were reapplied. Birds kept on long days without a rest on short days went through one testicular cycle and then remained quiescent. When continuous light was given, an initial spermatogenesis occurred, followed by involution. The testes after one spermatogenesis remained quiescent for 15 months after the start of this experiment. If, however, the continuous light was reduced to shorter days and then readministered, a new testicular stimulation took place.

These results indicate that 2 kinds of testicular quiescence occur in the adult. A reduction in day length produces an involution which is not characterized by a refractoriness to long day stimulation. If spermatogenesis is allowed to run its *full course* under long days then a refractoriness to long-day stimulation sets in. This latter refractoriness can be dissipated (at least for the Starling) only by a 'rest' on short days. For the Starling, there seems to be no inherent gonadal rhythm which can act independently of external light changes.

This latter type of testicular quiescence, i.e. that produced under long days, is here designated as true refractoriness.

In the research of Rowan (1929), Miyazaki (1934), and Damste (1947), the extra cycles perhaps occurred only because true refractoriness was not allowed to develop. Short days caused the gonads to involute before true refractoriness was established. It should be emphasized again that the research on the Starling indicates that the refractory phase of the gonadal cycle is influenced by light just as much as is the phase of progressive spermatogenesis.

For the Starling the natural end of refractoriness has not been determined, although it does end before mid-November at Hartford, Conn. Rowan (1929) first noted that the refractory period ends gradually. Riley (1936), confirmed by Kendeigh (1941), found that for adult English Sparrows, the refractory period ended before November 18. Miller (1948) with adult and immature Golden-crowned Sparrows determined the end between November 5 and 20. Wolfson (1945) with Oregon Junco (3 adult and 8 immature) got no response to light begun on October 18. A few White-crowned Sparrows did respond at this time. Rowan (1929) for Slate-colored Juncos got complete spermatogenesis with lighting begun November 1, and a slight response from October 2 lighting. For immature English Sparrows Riley (1936) got stimulation starting at September 30. Miller got no response with the Golden-crowned Sparrow from October 10 lighting. Schildmacher (1938) got sperm in immature *Phoenicurus* only when lighted about October 25, not earlier. Of course, date of hatch must be considered, since early hatched juveniles would be expected to mature before late hatch birds. The above figures indicate for the species mentioned a good deal of similarity for the time of ending the refractory period in the adults.

Miller (1948) continued his lighting until April. He observed that birds that did not respond to long days when tested early in the fall never did show testicular development. Interpreted in the light of our results in the Starling, it would seem that the long days prolonged the refractory period, which had not yet 'worn off'.

It is worthwhile to elaborate further on the results secured by Damste (1947) on the Greenfinch. His birds were activated by natural spring day lengths in the laboratory. In mid-May, before a natural testicular involution occurred, the birds were placed on very short days until August 14, when they were exposed to natural day lengths for that season in Holland. A new spermatogenesis resulted, followed by an involution which began about November 4, and which was completed by early December. In early December, artificial long days were given and a third spermatogenesis induced. These results are explicable in this wise: The 2 involutions were produced by short days, one artificially, the other naturally. These short days prevented true refractoriness from developing. After each involution, the birds were able to respond to longer

days. It is interesting to note that late summer and early fall day lengths are sufficiently long to be stimulating for the Greenfinch, provided the bird is not in a refractory state. To put it another way, some birds do not breed in the late summer because they have bred in the spring. Bissonnette (1937) seems to have been the first to discuss refractoriness as the limiting factor of reproductive periodicity.

Brown and Rollo (1940) kept Weaver Finches in nuptial plumage for more than a year by continuous long days. Rollo and Domm (1943) found that both short days and long days retarded the appearance of nuptial plumage. These findings show that inherent periodicity requires the cooperation of external day lengths. One must remember that plumage cycles and sex cycles are not the same thing. Testicular activation and the appearance of nuptial plumage are more or less congruent in this example.

For the Starling, it seems that day lengths affect the whole seasonal cycle, and do not merely fire an internal mechanism which, once set off, is self-controlling.

The question arises as to how the pituitary is inactivated internally. Miller (1949) demonstrated that the inactive testes of adult and immature Golden-crowned Sparrows could be activated by the injection of pregnant mare serum. This suggests that failure of testicular response is not due to a refractoriness of the testis. Riley and Witschi (1938) found that male English Sparrows responded equally well at all seasons to injected gonadotropin. Females, however, showed a seasonal response to the same treatment.

Witschi and Miller (1938) showed that both sexes of the Starling formed male and female sex hormones. Either or both of these hormones might depress the pituitary. For the domestic fowl, Riley and Fraps (1942) have tentatively suggested that the "gonadotropic content of the pituitary would . . . be inversely proportional to the sex hormone concentration . . . it is probable that the gonadotropic content of the hen's pituitary is influenced by more than one factor." Pfeiffer and Kirschbaum (1941) have suggested that androgen may cause a release of gonadotropic hormone in the female English Sparrow.

Burger (1944, 1945) found that testosterone neither blocked photoperiodic stimulation nor depressed an already activated testis in the male Starling. Estradiol had a disruptive, unnatural effect on the testis, but, when given with testosterone, this effect was abolished. Burger (1947) suggested that the testis does not give off a substance which inhibits the pituitary.

Witschi and Fugo (1940) found that testosterone did not have a depressing effect on the ovary of Starlings. Ringoen (1940) found that theelin had no depressing effect on the ovary of the sexually inactive female English Sparrow but that depression did occur in the activated ovary. Unpublished data (Burger) for estradiol in the female Starling confirm Ringoen.

The evidence thus far does not indicate that testicular involution and in-

activity in the adult male is due to a hypophyseal inhibition induced by male or female sex hormones. The situation in the female is more ambiguous. In the Starling, the bills of both sexes darken after the breeding season, indicating a low level of male hormone. Since a reduction in day length is enough to produce testicular involution in several species, there seems no need to suppose that some inhibitor is given off by the testis. The female exhibits 2 cyclic reproductive phases: (1) seasonal gametogenesis on which is superimposed (2) shorter cycles of ovulation. The fact that egg laying can be prolonged by merely removing an egg from the nest could be taken to indicate a limited role of the sex hormones in framing seasonal rhythmicity. Avian endocrinology has developed such an extensive literature that a review of other endocrine factors can not be condensed into this summary.

EXPERIMENTAL STUDIES OF BREEDING

When captive wild birds are subjected to photoperiodic manipulations, the females with few exceptions fail to lay eggs, but the males form sperm. Male Starlings which have been activated by light do not attempt to copulate with females, and there is a marked failure of the sperm to leave the testis. Cole (1933) seems to have been the first to induce a captive wild bird (the Mourning Dove) to breed by the manipulation of light. Benoit (1935) secured eggs from light treated immature ducks. The Black-crowned Night Heron has been stimulated to breed in the laboratory under light treatment (G. K. Noble, personal communication). Several other species have been induced to breed by light manipulations, and numerous species have bred or ovulated spontaneously in captivity.

It has been frequently suggested that psychic factors probably are involved for those species which do not breed under experimental conditions. A striking example of a psychic factor is given by Emlen and Lorenz (1942). Sexually inactive California Valley Quail were stimulated to mating behavior, apparently through contagion, i.e. the behavior of birds treated with sex-steroids affected non-treated birds. In ornithological literature, there exists a mass of descriptive, observational, and experimental data on the supposed and actual external factors and behavioral patterns existing at the breeding season. Little information exists, however, for the whole female sexual cycle of any one species, except for the common pigeon and the domestic fowl.

Polikarpova (1940) succeeded in inducing caged English Sparrows to lay eggs. The following factors were found: "Lengthening of the daily period of light stimulates the gland of the female up to a certain stage. The presence of the active male advances the development of the sexual gland of the female by one stage. For complete maturation and for egg laying the presence of nests is necessary." (p. 95). Polikarpova's results are compressed into a short paper; the size of the cages and the nature of the nests are not given. Except

in one case, it is not clear whether the Sparrows were allowed to build their own nests, or whether they were presented with prefabricated nests.

For the female Starling, I have accumulated a good deal of experimental data. When only females are caged together, long days induce a substantial development of oocytes. As with the male, the gonads regress if the long days are continued, and regress more rapidly if short days are given. If a number of males are caged with a number of females, ovarian development under long days is no better than with females alone. Much larger oocytes (two-thirds of ovulating size) were secured under the following complex: the daily light ration was increased gradually; birds were caged in pairs; nest boxes and nest material were provided. Isolation in different experiments of the following factors indicated that each *alone* is no more effective than light alone: the presence of the male; song from males not visible to the females; nest building; daily agitation of the cloaca for 12 days; insertion in cloaca of a macerated sperm-filled testis, with or without supplementary injections of estradiol. The aerial chase preceding the natural copulation of the Starling probably makes the laboratory breeding of this bird difficult or impossible, except perhaps in a large aviary.

Glass and Potter (1944) found that reduced lighting in the spring inhibited egg laying in the Quail. Hale (1946) temporarily suppressed egg laying in the summer in the domestic hen by the use of one hour of daily light filtered through a blue glass. The depression produced by the blue filter was more marked than that produced by restricted feeding.

It should be emphasized again that egg laying or its failure gives only partial information on the condition of the ovary. Failure to ovulate may mean that only the terminal stages of ovarian activity are lacking. For example, I have caged egg laying Starlings, which on autopsy possessed full-sized ovarian oocytes. Rarely, however, did one of these females lay an egg. On the other hand, it is well known that in some species, the removal of an egg from the nest will induce the laying of an extra egg. In poultry, the disruptive effect of the cock on egg laying is well known.

Kendeigh (1941) found that House Wrens under cooler conditions produced larger clutches and larger eggs than at the peak of the breeding season. Schooley and Riddle (1944) by light were able to modify the spacing of the two eggs of a clutch of Ring-doves. Fraps, Neher, and Rothchild (1947) placed domestic hens under continuous light, and then by restricted feeding were able to control the time of ovulation. These activities, however, are terminal events which occur in a previously activated ovary. The results of Fraps, et. al. do not demonstrate that reproduction in the hen is solely conditioned by feeding time.

By the use of appropriate gonadotropins, a successful ovulation has been obtained in the hen (cf. Fraps and Riley, 1942 for details and bibliography). This is apparently the first complete ovulation secured by hormonal treatment.

A sexual difference in response to a level of gonadotropin is seen in the work of Kirschbaum, Pfeiffer, Van Heuverswyn, and Gardner (1939) on the English Sparrow. The ovary during long days remained relatively inactive, but immature testes transplanted into these females formed sperm. This may mean that the gonadotropin output under the light stimulus is the same for the 2 sexes in the Sparrow. The female may get the additional output of gonadotropins necessary for the ovarian cycle by other, non-photic stimuli (cf. Polikarpova's results). It may be that non-light stimuli can raise the gonadotropin output in the male. I have tested several times the testicular response of Starling males caged with males, and males caged with females. There seems a slight added effect produced by the presence of the female. It will be noted that in the female Starling, light alone brings the ovary up to the point of readiness for the later growth changes, i.e. perhaps to the point where additional gonadotropins that are not stimulated by light must be added. This may clarify formulations about the influence of light in the female.

CONCLUSIONS

The experimental data are yet too fragmentary to explain seasonal reproductive rhythmicity the world over, if indeed a single unified theory is possible. Genetic selection in poultry has been able to modify reproductive rhythmicity, giving evidence that natural selection has utilized the genetic variability from which species differences can be built. There is no evidence for any species of bird that its reproductive rhythmicity occurs independently of controls in the external environment. In certain species, at least, there is a difference in the factors effective in the two sexes.

All truly wild species of birds tested have been influenced to some degree by photoperiodic manipulations. How light effects pituitary stimulation is largely unknown. The theory as currently phrased, that light acts indirectly by promoting increased hypothalamic activity through longer bodily activity or wakefulness, stands "not proven". The alternative view that light acts in a less indirect fashion has more experimental substantiation, but it too is "not proven". The influence of other environmental factors beside light are most obscure. Likewise, little is known as to the relation of psychic factors to gonadal state. Most of the birds tested are native to the northern hemisphere, and either are not migrants or do not migrate deep toward the equator or trans-equatorially. Several annual spermatogenetic cycles have been produced in the laboratory for both resident and migratory birds by photoperiodic manipulations. Modification of the plumage and the testicular cycle of one tropical bird has been reported. This reviewer is not a partisan of the photoperiodic theory, he merely states that photoperiodic changes are the only widely spread factor capable of modifying reproductive rhythmicity which is moderately well-known through experimental testing.

Attention is called to the idea that in seasonally reproducing birds, sexual activation can occur only when a refractory period has been experienced and dissipated. This refractory period can be modified, in some species at least, by photoperiodic manipulations, just as the progressive phases of the cycle can be modified by light. Long days effect a persistence of the refractory phase, and short days favor its dissipation. It can be suggested that when the relation of the refractory phase to environmental conditions is understood more precisely, reproductive rhythmicity will be better understood. Attention has been focused too narrowly on the progressive phase of the reproductive cycle.

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