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*REPRODUCTIVE CYCLES IN AN EQUATORIAL SPARROW**

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The male avian reproductive system undergoes cycles of activity in which there are periods of reduced, nonfunctional gonads alternating with those when the active testes are 150 times the size of the resting stage. Such cycles occur in essentially all wild species that have been investigated. Control of the cycle by the gonadotropic hormones of the pituitary has been demonstrated, a control that parallels the especially well-documented situation in mammals of pituitary regulation of reproductive periodicity.

In every instance in birds in which manipulation of the cycle has been attempted by experimental light treatment, it has been found that greater day length stimulates the pituitary-gonad mechanism. On the other hand there are periods following maximum activity, and also periods in the maturing of individuals, when the mechanism is refractory to the normally stimulating effects of light increments. These seemingly necessary periods of rest and organization have a strong tendency to alternate with recrudescent phases and constitute the basis for ascribing an innate rhythmic attribute to the mechanism. The general conclusion has been drawn that the annual reproductive cycles of species of temperate and high latitudes is the result of this general rhythmic tendency coerced by seasonal photoperiodism so that the onset of the breeding season is precisely timed in adaptation to the average annual development of favorable ecologic conditions for the species; the breeding effort that ensues thus can achieve maximum success.

As one examines species living at progressively lower latitudes, where seasonal photoperiodism is less extreme, many instances of the influence of factors other than day length become apparent. Thus even at latitude 38° some species have breeding seasons during the shortest days of the year in adjustment to rainfall patterns and the related plant and insect food sources.[1] In a few instances at least the actual or proximate stimuli to recrudescence have been traced to factors such as flowering of plants or availability of plant growth[2] or to the onset of rains. These stimuli other than light are best revealed in desert areas where they are variable in timing from year to year and where recrudescence therefore cannot possibly be keyed to any phase of photoperiodism.

Nevertheless the prevailing influence of photoperiods is detected, through critical correlations, in an equatorial direction as far as latitude 10°N where most species breed during the longer days of the year following the vernal equinox.[3] This is true both in wet and dry belts and among species that are partly influenced by seasonal moisture conditions.

In equatorial latitudes, between 5°N and 5°S, the photoperiod fluctuations are so reduced as to have no physiologic effect on reproductive rhythm. One may expect, then, (1) that innate cyclic tendencies will be expressed in some species without the coercion of photoperiodism, (2) that such species may as species show continuous breeding because the normal variability in length of the presumptive individual cycles would put these individuals out of phase with respect to one another, and (3) that other species that inhabit areas with strong rainfall cycles will be coerced into exhibiting coordinate, restricted breeding seasons by evolving sensitivities to some one of a variety of proximate stimuli arising directly or indirectly from rainfall.

As a result of previous work in Colombia, South America, at equatorial latitudes in an area with weak rainfall cycles, it was found that in eight of ten sample species breeding condition in males could be encountered in all segments of the year.[4] But we discovered also, as evidence from equatorial Africa had already partly shown,[5] that adult males of these species undergo testis regression to a point fully equivalent histologically to the state of winter dormancy of north-temperate birds. It was thus evident that individuals underwent some type of cycle even in the continuously breeding species.

The purpose of the investigation of 1958 in Colombia was to ascertain in such a continuously breeding bird the number of cycles and the duration of each phase of

the cycle in a given individual through a twelve-month period. The species selected for study was *Zonotrichia capensis*, a congeneric relative of the North American Sparrows of the genus *Zonotrichia* on which much of the experimental work on photoperiodism and breeding physiology has been conducted.[6, 7, 8] To achieve significant results on *Zonotrichia capensis*, free-living individuals marked for identification needed to be followed by means of observation and by periodic recapture to ascertain the occurrence of stages of testis enlargement and regression.

Methods and Procedure.—A research station was established in an area of dense population of *Zonotrichia capensis* on the crest of the Western Andes, 6,500 feet elevation, west of the city of Cali, Colombia, at latitude 3°30'N. This research center was maintained from February 8, 1958, to January 23, 1959. In the course of the year 160 individuals were captured and individually color marked on an area of four acres. The most critical results were derived, however, from the subsequent history of the first 50 birds captured in the initial three weeks. These latter consisted largely of resident adult and postjuvenal individuals, in which there was good survival, of about 78 per cent, through the ensuing ten or eleven months.

Breeding level in males is regarded as a stage of testis development in which mature sperm are present either in bundles or free in the lumen of the seminiferous tubules. If sperm are not free, it may safely be assumed that they can be so freed within five to ten days under the stimulus of courtship and nesting behavior of the pair and that the male is therefore in potential breeding condition. In the regressed testis spermatogonia and primary spermatocytes are present but only a few of the latter show synapsis of the chromosomes. By correlation studies of the linear dimension of the testes and microscopic sections carried out on birds collected in areas adjacent to that occupied by the living marked population, it was determined that testes 6 to 9 mm in length are in potential breeding condition and that testes 1.5 to 2.5 mm in length were in inactive state. Testes 2.5 to 5.0 mm in length if they are firm or turgid are in various stages of the maturation divisions which implies a prior period of inactivity. The decline from active state is very rapid and the testis in this transition is soft and usually distinctively yellow.

Further correlation studies among the 80 birds autopsied showed that a cloacal gland development represented by external diameters of 5 to 8 mm of the cloacal protuberance invariably reflected a testis in potential breeding condition. Moreover, birds that were engaging in steady territorial defense song always possessed an active testis. The converse situations, however, did not hold. Reduced cloacal glands and absence of song may at times accompany a fully enlarged testis.

A critical procedure was the recapture of individuals and the performing of a laparotomy whereby the internally situated testis could be measured with calipers. Following closure of the abdominal wall and recovery from anesthesia the bird, within an hour, could be returned to the field, where it would at once resume its singing and nesting behavior if it were in an active state. This operation was performed as many as three or four times on some individuals without any ill effects and it was particularly important in establishing periods when the testes were in regressed or early recrudescent stages. The uncertainties of survival in the wild and of recapture at the proper periods for laparotomies were factors on which we gambled but with which we had good fortune.

Age determination of individuals was made by observing presence and progressive disappearance of the ventrally streaked juvenal plumage. All identifiable remnants of such plumage are lost by 80 days of age. Up to eight months of age, and occasionally to ten months, evidence of immaturity persists in the skull in the form of progressively reduced areas of translucent bone in the frontal region; these "windows" are later closed through full separation of the two layers of this bone by an air space and supporting trabeculae. This skull area may be repeatedly examined by operating without anesthesia to slit the thin overlying skin and expose the bone; suturing with scotch tape permits immediate return of the bird to the field. Age in the period from three to nine months can thus be gauged approximately by measuring the size of the frontal "window."

By correlation of all evidence derived from operations, external features of the plumage and the cloaca, and behavior involving song, copulation, and actual participation in nesting, the reproductive state could be ascertained in a number of males over a ten to twelve months' period.

Results.—The evidence indicates a full reproductive cycle, involving one high and one low point, of five to seven months' duration, the normal length being six months. Case histories of 29 postjuvenal and adult males that reflect status over a period of six months or more in no instance offer the slightest suggestive evidence of appreciably longer cycles. Moreover, the like records of 27 females in no instance show sustained breeding activity for more than six months without rest periods.

The positive record of cycles in males consists of 17 timed cycles attested by laparotomies for the low points and by laparotomies and/or positive cloacal or behavioral evidence for the alternating high points. There are five additional cycle records for which the evidence for the low points is indirect, consisting of conspicuous cessation of song and/or heavy involvement with molt.

The most decisive records are those derived from five males in which two complete cycles were traced, thus clearly demonstrating the double cyclic situation for the annual period. The records of these are summarized in Table 1. Herein the

TABLE 1

RECORDS OF CYCLES OF FIVE WILD MALES OF *Zonotrichia capensis*

Individual	High	1st Low Point	High	2nd Low Point	High
466	C	Mar. 2	L, C, N	Aug. 25	C, N
472	...	Mar. 20 (Apr. 7)	L, C, N	Aug. 26	C, N
480	L, C	Mar. 16	L, C, N	Oct. 20	C
484	L, C	Mar. 20 (Apr. 8)	C, N	Nov. 3	...
806	...	Mar. 8	C	Sept. 8	C

critical low points are determined by laparotomies. If the operation revealed a testis in middle stages of recrudescence, the low point was extrapolated from this and the actual date of the operation placed in parentheses. The fully resting testis state is apparently maintained for only two or three weeks at most and thus serves as a convenient reference point. The alternating periods of full breeding potential are attested in these birds by laparotomies (L), and/or greatly enlarged cloacal protuberances (C), and participation in nesting (N).

The length of the sustained breeding condition or plateau was determined rather closely in ten adult birds. These are best expressed as minimum durations

based on positive evidence. They range from three to six months, but eight of the ten are in the range of 3 1/2 to 4 1/2 months. Maximal possible periods might be estimated by extrapolation from intervening lows but would in no instance be more than two or three weeks greater than the proved minima.

In immatures undergoing their first testicular enlargement, the plateau may be shorter. In one instance it was proved to be only 2 2/3 months and similar short durations were suggested purely by behavioral evidence in several other immature individuals. Such short plateaus were never found in adults.

The interval of rest could be measured only as the gap between the end of one high plateau and the beginning of the next, owing to the rapidity of regression and the briefness of actual rest (less than a month) and recrudescence. To ascertain and time the progress of these rapid changes would have necessitated more frequent captures and operations than the circumstances and the recovery of the birds would permit. The maximum time for the regression and recovery interval ascertained from six histories ranged from six weeks to three months, the latter probably longer than real; the normal period was two months.

The age in months at which young males first attain breeding condition was found to be as follows in seven individuals with adequate records: 5, 6, 7, 7 1/3, 8, 9 1/3, 11 1/3. There is a very small chance that in the last two instances a very brief recrudescence and subsidence could have occurred short of nine to eleven months and been undetected but it could not have been of such duration as actually to have permitted nesting. Although we were not fortunate enough to find any of these particular males actually engaged in nesting, two females at calculated ages of 4 1/2 and 9 1/2 months had laid clutches of eggs. In the first instance if we allow for some delay in initiating or completing the postjuvenal molt beyond the normal chronology, the age of breeding might have been five months, but not more.

To be detailed in another paper are full data on weather and on the statistics which show when the largest numbers of individuals are at breeding level. Briefly it may be indicated here that the modal occurrences of breeding fall in May, June, and July and in December, January, and February. These months represent the ends of the wetter seasons and the early parts of the ensuing drier periods; the heaviest rains are in April and May and in late October, November, and December (Table 2). Thus the peaks of breeding are related to and in some

TABLE 2

WEATHER RECORD AT 4 KM NW SAN ANTONIO, 6,500 FT, VALLE, COLOMBIA
Monthly averages of maximum and minimum temperature (°F) and total rainfall, February 8, 1958 to January 23, 1959

	Minimum	Maximum	Rainfall, in.
January	57.9	70.0	1.1 (23 days only)
February	58.5	71.5	3.065 (20 days only)
March	58.6	72.9	5.51
April	58.2	71.4	7.37
May	58.7	72.1	8.05
June	58.6	73.8	1.13
July	57.8	72.5	1.29
August	57.6	73.4	3.47
September	57.3	72.7	1.16
October	56.9	70.7	7.60
November	56.7	68.6	4.95
December	56.7	68.4	6.49
			51.23 (1 yr. less 15 days)

way induced by the rainfall cycle but not by the weak traces of photoperiodism, for it is to be observed that one peak spans the summer solstice (for 3 $^1/_2$°N latitude) and the other the winter solstice. It should be re-emphasized, however, that birds in breeding state and successful nesting occur in every month of the year.

Conclusion and Summary.—In equatorial species of birds that exhibit potential breeding state at all periods of the year, individual males undergo cycles with maxima and minima equivalent in degree of difference in physiological level to those of their temperate zone relatives. In one such species, *Zonotrichia capensis*, the first of its kind to be studied intensively, the cycles of the individual average six months in duration and two complete cycles are manifest each year. The high plateau of breeding potency in males normally lasts four months and the intervening regression, rest, and recrudescence of the testis occupies two months.

The six-month cycle in *Zonotrichia capensis* is an expression of innate cyclic tendency. It is uncoerced by small variations in photoperiod and is only incompletely controlled by the seasonal occurrence of rainfall, which however does appear to induce a majority of the population to engage in breeding in the late parts of each of the two wetter periods of the year.

Young males attain the breeding plateau at five to eleven months of age. Young females may actually engage in nesting when five months old.

The variable age of attainment of breeding potential and the individual variability of the innate cycle of the adult males is responsible for the production of some young in every month of the year.

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