VERNAL TESTES DEVELOPMENT IN TROPICAL-WINTERING DICKCISSELS

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SINCE 12-hour daylengths experienced by tropical-wintering species are stimulatory to the hypothalamic—hypophyseal—gonad axis of temperate-wintering species (Burger, 1953; Dolnik, 1963; Farner, 1961; Wolfson, 1960), the question of why these migrants do not complete gametogenesis during the several months' stay on their contranuptial area has been of interest (Marshall, 1960; Wolfson, 1959*a*). It can be assumed that different tropical migrants could adapt the regulation of their annual cycles in a number of different ways or by a combination of different mechanisms in order to be successful in their specific environments.

One possibility was suggested by Wolfson (1959*b*) who hypothesized that these migrants might respond to 12-hour daylengths at a slower rate than temperate species so that gametogenesis cannot be completed until they are exposed to the longer daylengths of their temperate breeding grounds. This hypothesis is indirectly supported from work done on temperate species which has shown that the rate of testes growth is proportional to the length of the photoperiod (Lofts, Follett, and Murton, 1970) and hence birds wintering at tropical photoperiods might be expected to have even a slower rate of testes development. Another possibility could be that the refractory period of tropical-wintering species is longer than that of temperate species and thus they cannot begin to respond to photostimulation until just prior to the northward journey (Marshall, 1959). Both these hypotheses receive indirect support from the observation that gonad growth begins for tropical migrants on the winter range, but it does not appear to progress very far (Rowan and Batrawi, 1939; Marshall and Williams, 1959).

Lofts and Murton (1968:350) stated that "birds that are photosensitive to medium northern daylengths have had to evolve adaptations if they migrate to near or across the equator, in particular they require to have long refractory periods and a slow response to stimulatory daylengths once they are out of the refractory phase." As far as we know, however, this generalization based on the hypotheses of Wolfson and Marshall has not been supported by any direct evidence.

The Dickcissel (*Spiza americana*) breeds in temperate North America and winters in the Neotropics north of Amazonia. Although we have not shown that there is a relationship between this species' natural photoperiod experience and the regulation of its annual gonadal cycle, Morrison (1971) has demonstrated in post-breeding adults that after approximately 8 weeks exposure to a 12-hour photoperiod (around mid-November), precocial gonadal development can be stimulated by the 15-hour photoperiod that they would experience on the breeding grounds. These results show that a 12L-12D photoperiod regime will terminate photorefractoriness in the Dickcissel and that the length of its refractory period is similar to that of many Temperate Zone species (Farner, 1959; Shank, 1959; Wolfson, 1958). It seems, therefore, that a prolonged refractory period is not the mechanism this species uses to prevent the development of the reproductive state while on the wintering grounds.

The following data on the rate of testes growth and the magnitude of the response in wild birds living under their naturally-occurring photoperiod are presented to test the slower rate of response hypothesis.

METHODS

Male Dickcissels were collected from wild populations on the wintering grounds in Panama and the Canal Zone (9° N) from 19 January through 2 May 1961, and the length of each testis was measured in millimeters. The daylengths during this period of collection ranged from 11 hours, 40 minutes to 12 hours, 28 minutes. Similar data were obtained on the breeding grounds in Illinois (40° N) from birds collected during May, June, July, and August in 1961 and 1962.

In order to convert testis length into weight, Morrison in the course of his work on the refractory period measured the length of the testis and then after treatment according to the methods used by Wilson (1968), obtained their weight in milligrams. He calculated the following relationship:

$$\log \text{testis wt. (mg)} = -0.5845 + 3.0696 \log \text{testis length (mm)}.$$

In the quantification of the gonad growth rate from data collected by photostimulation of receptive birds under laboratory conditions, the time axis is calibrated according to days since the beginning of exposure to the stimulatory photoperiod. This, of course, is not possible with a free-living population, since day zero is not known. In order to calculate k, the logarithmic testicular growth-rate constant (= slope of the time $\times$ log weight regression), the logarithm of the combined weight of both testes was plotted against the date of collection. Then the linear portion of the curve was identified by inspection, and 28 February was selected as day 1. A linear regression of the logarithm of the combined testes weight as a function of time was computed through 2 May as day 64. The natural photoperiod during this period ranged from 11 hours, 56 minutes on day 1 to 12 hours, 28 minutes on day 64, averaging 12 hours, 13 minutes.

RESULTS

Figure 1 is a semi-log plot of the combined testes weights according to the date of collection. Even though Dickcissels will respond under experimental exposure to 15 hours of light in mid-November, under the natural photoperiod conditions of their wintering grounds the testes are still small in January.

This figure also includes the linear regression calculated for the period from 28 February through 2 May, which is expressed by the following equation:

$$\log \text{wt.} = 0.2757 + 0.03114\ t,$$

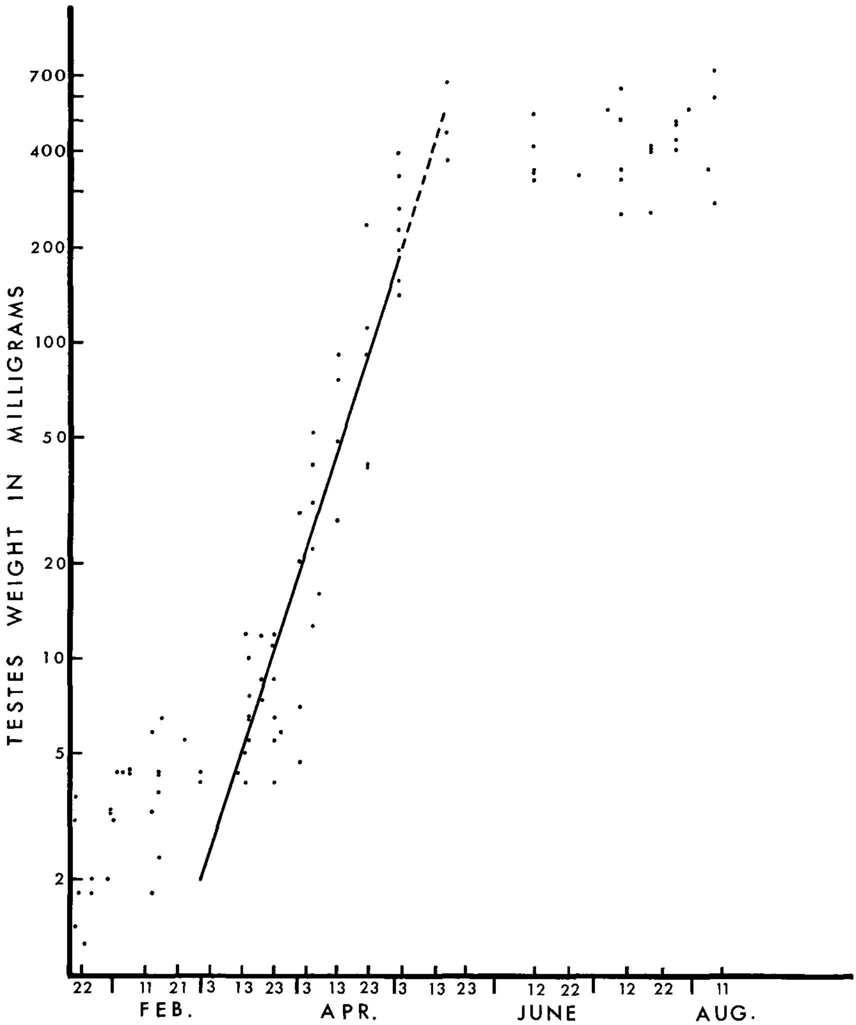

FIG. 1. Combined testes' weights of wild Dickcissels collected on both the winter and summer ranges.

in which "wt" is the combined testes weight in milligrams and "t" is in days, beginning with 28 February equal to day 1. The logarithmic testicular growth-rate constant, k, is thus equal to 0.03114 day^{-1}. It is also apparent that a growth rate of this magnitude will lead to testes of breeding size by the time the population migrates to and becomes territorial on its breeding range in mid-May (dashed extension of linear regression in Figure 1).

The average weight of the combined testes in Illinois is 439.23 ± 21.77 mg (SE, n = 28). Birds collected in June and July had swollen seminal vescicles, indicative of the production of spermatozoa. Even the bird collected on 19 July whose combined testes weight was only 256 mg was producing sperm. Finding functional breeding testes of such a wide range in size apparently is not unusual (Dolnik, 1963).

DISCUSSION

The temperate-wintering White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) has a *k* value for adult males on a 12-hour photoperiod equal to 0.0225 (Farner and Wilson, 1957). If the same ratio between growth rates of first year birds and adults that occurs in the White-crowned Sparrow (*k* of first year males = 1.16 k of adults) is valid for adult Chaffinches (*Fringilla coelebs*) then the *k* of first year males which equals 0.0213 in this temperate species has a value of only 0.0184 in adults at a 12-hour photoperiod (Dolnik, 1963). Both these values are less than the 0.03114 computed for the logarithmic testicular growth-rate constant in the Dickcissel at a 12-hour photoperiod, and therefore the slower growth rate hypothesis is rejected for this tropical-wintering species.

Hamner and Stocking (1970) have similarly rejected both the prolonged refractory period hypothesis and the slow growth rate hypothesis for a trans-equatorial migrant, the Bobolink (*Dolichonyx oryzivorus*).

The question therefore still remains open as to why the testes do not begin to develop earlier than they do. The energy resources of the environment do not appear to be the main limiting factor. Although the prenuptial molt is typically completed prior to the onset of gonadal growth, the development of the testes is coincident with fat deposition and migratory behavior (Zimmerman, 1965).

Hamner (1968) presents the following observations from his studies of the photoperiod control of the gonadal cycle in the House Finch (*Carpodacus mexicanus*): 1) the termination of photorefractoriness can be accomplished by daylengths as long as 14 hours or as short as 6 hours and in all cases the termination is completed in the same time interval, 2 months; 2) wild birds that *are* photosensitive in the autumn experience a daylength of 12 hours but show no gonadal growth while the same daylength does induce rapid gametogenesis in the spring; 3) the renewal of photosensitivity is a gradual process in that the long-day effect on birds in the fall is not as great as the same long daylength in the winter; and 4) using an interrupted night technique on photosensitive birds, there was a change in circadian sensitivity from October to January in that this period of photosensitivity shifted from 20 hours after dawn in the October birds to 12 hours after dawn in the January birds.

Hamner hypothesized that there are two components in the House Finch's refractory period. The first phase, the "absolute refractory period," follows immediately after breeding and is a period during which even continuous light treatment is non-stimulatory and whose duration is independent of the photoperiodic environment. The absolute refractory period is then followed by a period of "relative refractoriness" during which the bird initially is insensitive to daylengths equal to or shorter than those to which it had been previously exposed but this insensitivity is affected by the photoperiod regime it is experiencing so that as daylengths decrease in the fall there is a shifting of a threshold for stimulation until finally this threshold reaches a daylength less than that of the actual environment at that time and light again becomes stimulatory on the system.

On the basis of Hamner's (1968) suggested mechanism, we hypothesize that Dickcissels escape absolute refractoriness soon after their arrival on the winter range, but still remain in a state of relative refractoriness to the tropical photoperiod. Some time in February, as a result of the continued lowering of the photoperiodic threshold, Dickcissels are released from relative refractoriness and gonad growth begins.

Since we have not been able to illustrate in the tropical-wintering Dickcissel that there is a refractory period longer than that of temperate species or a slower rate of testes growth in response to the naturally-occurring photoperiod in the spring than has been shown for temperate species, we suggest that there is no special adaptation for the regulation of its gonadal cycle because of its wintering at a latitude where it seldom experiences days of less than 12 hours duration. It, like temperate species (Wolfson, 1960), is simply specifically adapted to the photoperiodic environment it experiences as a result of its migratory behavior.

SUMMARY

Sizes of testes obtained from wild populations of the Dickcissel on its wintering range in Panama and the Canal Zone were used to compute a logarithmic testicular growth-rate constant, k, equal to 0.03114 day^{-1}. Since this value is not less than that of temperate-wintering species exposed to 12-hour photoperiods, the slower growth rate hypothesis is rejected for the Dickcissel.

Furthermore, this k value is great enough to lead to the development of breeding-size testes.

Since previously completed work by Morrison led to the rejection of the prolonged refractory period hypothesis, the question of why gonads of wintering Dickcissels do not begin their development earlier is still not answered. A mechanism based on the notions of Hamner (1968) is suggested as a hypothesis yet to be tested.

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NEW LIFE MEMBER

A new addition to the list of Life Members of the Wilson Ornithological Society is Dr. David F. Parmelee, one of the recognized authorities on bird life of the high Arctic. Dr. Parmelee is currently Professor of Biology and Chairman of the Field Biology Program at the University of Minnesota. He has made numerous expeditions to the Arctic and published approximately 50 papers on his observations there as well as two small books. Our picture shows him (with friend?) on one of these trips. Dr. Parmelee holds degrees from Lawrence College, and the University of Oklahoma. He is a member of the Cooper Society, the state ornithological Societies of Kansas, Oklahoma, and Minnesota, and an Elective Member of the AOU. Besides his scientific work he is also a skilled bird photographer and painter. Dr. Parmelee is married and has one daughter.