THE PHOTOPERIODIC TESTICULAR RESPONSE OF A TROPICAL FINCH, *ZONOTRICHIA CAPENSIS COSTARICENSIS*

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Among the North American members of the genus *Zonotrichia*, photoperiodic mechanisms are prominent in the control of annual gonadal cycles (Wolfson 1954, 1958, 1966; Farner and Wilson 1957; Farner 1966, 1967; Farner and Follett 1966). Of interest, with respect to the control of reproductive function in this genus, is the demonstration (Miller 1959, 1965) of a photoperiodic testicular response in an equatorial population of *Zonotrichia capensis* in Colombia. Because of this we have conducted the preliminary studies, presented herein, on a more northern population in Costa Rica.

In Costa Rica, *Zonotrichia capensis costaricensis* occurs at 500–3000 m, being most common at mid-elevations (Slud 1964; Skutch 1967; Wolf 1969). Within its range it is abundant in pastures and early, second-growth scrub; it is also the most common dooryard bird, even in large cities.

MATERIALS AND METHODS

Birds taken in the field for this investigation were obtained from two areas in Costa Rica. From 3 to 5 December 1966, 27 specimens (15 males, 12 females) were shot or netted in hedgerows in agricultural areas of the central plateau 8 km SW of the city of Cartago (ca. 10°N) at an elevation of about 1600 m. All birds were in flocks at this time, and there was no singing. Following fixation of gonads in Bouin's solution, they were transferred to 70 per cent alcohol for five days and then weighed. Later they were embedded, via tetrahydrofuran, in paraplast and examined histologically. The histologic stages of development are those of Blanchard (1964). Birds with fully pneumatized skulls were regarded as adult; others were designated as immature. The mean weight and standard error of the testes of nine adult males was 9.9 ± 2.2 mg; the testicular weights for the three immature males were 0.5, 0.8, and 1.4 mg. The developmental stages of the testes of the adults varied from stage 5 in the larger testes (23 and 31 mg) through regressing state to stage 1 in the smaller testes (0.9–1.8 mg). The testes of the immature males were in stage 1. None of the males was in molt. The mean weight of the ovaries of six adult females was 9.9 ± 1.9 mg; for two immature females the weights were 0.5 and 9.1 mg. The ovary of the third immature female was lost; this bird was in molt with developing feathers in the scapular tract and tail.

Sixty-four birds from unknown localities in Costa Rica were received in Seattle on 19 April 1967 via air from San José. They were held until 26 September under natural day lengths. On arrival in Seattle both males and females were in various stages of molt and gonadal development. All birds were in adult plumage. In a sample of seven males, testicular weight ranged from 5 to 213 mg (mean, 109 mg, excluding one male in heavy molt with the testicular weight of 5 mg). The four females in the sample were not in molt; weights of the ovaries ranged from 12 to 80 mg.

On 26 September exploratory laparotomies were performed on several individuals for estimation of gonadal weight and all birds were transferred to a daily photoperiod of 8 hr (8L 16D) until 6 November when a group of six (Initial short-day controls) was sacrificed. Two groups of six and seven, respectively, were then changed to 20L 4D and were sacrificed after 23 and 38 days, respectively (Long-day I and Long-day II). A fourth group of six, Final short-day controls, was retained on 8L 16D, and sacrificed 38 days later (see table 1). Liver and pieces of pectoral muscle were dried and weighed, then refluxed with dichloroethane and weighed after drying.

RESULTS

GONADS

Nine males laparotomized on 26 September had relatively large testes (mean of estimated weights, 176 ± 10 mg). The mean estimated weight of the ovaries of the five adult females was 54 ± 10 mg. When these gonadal weights are compared with those of the short-day control groups (table 1), it is clear that short days (8L 16D) caused gonadal regression and partial reactivation (up to stage 4–5) within less than 41 days, and that the development of the testes did not proceed beyond stage 4–5 for at least 38 days except in one case (F-4065) in which the 64-mg testes were at stage 6–7. Thus, short days did not prevent the maturation of the testes up to the formation of primary spermatocytes, but the final stages

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TABLE 1. The effect of long daily photoperiods on the testes of *Zonotrichia capensis costaricensis.*

Group	Photoperiodic regime	n	Wt., testes $\bar{x} \pm$ SE mg	Stage of development of testes
Initial short-day control	8 L 16 D, 42 days (26 Sept.–6 Nov.)	6	7.7 ± 1.6	2 in regression 2 stage 3 1 stage 3–4 1 stage 4–5
Long-day I	8 L 16 D, 42 days (26 Sept.–6 Nov.) 20 L 4 D, 23 days (7 Nov.–29 Nov.)	6	112.5 ± 21.8	1 in late stage 6 1 in stage 6–7 4 in stage 7
Long-day II	8 L 16 D, 42 days (26 Sept.–6 Nov.) 20 L 4 D, 38 days (7 Nov.–14 Dec.)	7	206.7 ± 14.3	all in stage 7
Final short-day controls	8 L 16 D, 80 days (26 Sept.–14 Dec.)	6	18.9 ± 9.5	1 in stage 2 2 in stage 4 2 in stage 4–5 1 in stage 6–7 (64 mg)

of spermatogenesis remained to be induced by long days. The advanced development of the testes of F-4065 suggests the possibility of an endogenous cycle that can override the effects of short days, but this requires further investigation. If a photorefractory period exists in adult males of *Z. capensis costaricensis,* it must be shorter than 64 days since the gonads of the birds in Long-day I (23 days) showed a strong response to photostimulation by increase in weight and development (stages 6 and 7). The histological findings indicate the maximal spermatogenesis was attained before 38 days of 20L 4D (table 1). Compared with the gonadal growth-rates of photostimulated *Z. leucophrys gambelii* (Farner and Wilson 1957), it appears that our experimental *Z. c. costaricensis* showed a slower rate of testicular growth. Assuming logarithmic growth during the first 23 days of photostimulation, the growth-rate constant would be about 0.05 days^{-1}, compared with 0.08–0.11 days^{-1} for *Z. l. gambelii* (Farner and Wilson 1957), depending on photosensitivity (Farner and Follett 1966).

BODY WEIGHT AND LIPID DEPOSITION

We found no response in the body weight to the alterations in the photoperiod, despite the fact that the livers of the Final short-day controls contained more fat (28 per cent of dry weight) than did those of the birds in Long-day II (17 per cent dry weight); the corresponding values for pectoral muscle were 10.2 and 12.7 per cent, respectively. The almost constant body weights in both experimental groups, together with the observations on the adipose tissue, indicate clearly that the changes in the gonads of the experimental birds are a photoperiodic effect and not the result of more favorable nutrition associated with longer days. We offer no explanation for the apparently higher hepatic lipid level of the short-day birds. The absence of a photoperiodically induced increase in weight is consistent with the absence of such in the non-migratory *Zonotrichia leucophrys nuttallii* (Farner 1960).

DISCUSSION

The breeding season at Vara Blanca has been investigated by Wolf (1969). At this locality (10° 10′N) the difference between the longest and shortest days is about 76 min. The climate is generally cool and wet, with a dry season from February through April and a shorter period of reduced rainfall in July and August. The months of heaviest rainfall are usually May–June and September–November. Mean monthly temperatures range from 15.4 to 17.4° C. Evidence from gonads, brood patches, molt, and presence of eggs and young, indicate that at this locality there is a major breeding period from February to May (sometimes to June), followed by a molt and then a second, though lesser, breeding period in July and August (Wolf 1969; see, also, Skutch 1967).

In the Cartago area, where the birds were collected in December 1966, the breeding period appears to be similar. Birds were in molt at Laguna de Coris, the major collecting site, on 10 July 1966, but there was much singing on 19 August and several pairs of birds behaved as though they had active nests. There were no indications of breeding activity on 5 October and the birds remained in a non-breeding state, at least through early February. Birds are in full song throughout the central plateau of Costa Rica from February through June.

The observations of Wolf (1969) and Skutch (1967) suggest that, despite the two "breeding seasons," apparently separated by a molt, at least some nesting may occur in every month of the year, a situation similar, perhaps, to that observed by Miller (1955, 1962) in Colombia. Further north in Guatemala, Baepler (1962) reported a breeding season with two maxima, suggesting that the fall season was more extensive, and correlated with the heavy rains. In southern México, Wagner and Müller (1963) have reported a single, somewhat protracted season.

When equatorial *Zonotrichia capensis* from Colombia were held at 38°N in Berkeley, the natural long days of this latitude (up to 15.25 hr) apparently caused an abnormal extension of the reproductive period from four months to 7–10 months (Miller 1965). In a similar manner the consistently relatively large gonads of our birds, held on the natural photoperiods of Seattle, appear to be the result of a photoperiodic gonadal control mechanism.

In the light of our findings, it seems very likely that not only adult females (Miller 1965), but also adult males of the equatorial *Z. capensis* undergo gonadal regression when subjected to short daily photoperiods. The failure by Miller (1965) to obtain testicular regression in his colony of equatorial origin could be due to the fact that his "short days" of approximately 10 hr were not short enough to be effective for males although they were for females.

At this point it should be recalled that, at least superficially, similar photoperiodic gonadal responses have been reported among other equatorial or low-latitude species (Brown and Rollo 1940; Rollo and Domm 1943; Marshall and Disney 1956; Disney et al. 1961; Lofts 1962; Thapliyal and Saxena 1964; Thapliyal and Tewari 1964; Thapliyal and Chatterji 1965). Unfortunately, in no case has the significance of these mechanisms been subjected to a quantitative examination such as has been applied to *Zonotrichia leucophrys gambelii* by Farner and Wilson (1957), and to three palearctic fringillid species by Dolnik (1963). Clearly, however, natural photoperiod cannot be the controlling information in equatorial populations such as those of *Quelea quelea* and *Zonotrichia capensis* studied by Marshall and his colleagues, and by Miller, respectively. Although we agree with Wolf (1969) that photoperiodic information may be of little importance in the battery of information that controls the annual cycle of *Zonotrichia capensis* in Costa Rica, we feel that a final decision must await careful laboratory experiments involving, in part, daily photoperiods natural to the population. Temporarily at least, we must set aside his argument, based on later breeding at 2200 m than at Vara Blanca (same latitude, 1800 m). The two populations could well have had genetically different "interpretations" of the same day lengths (as Dolnik 1963 has demonstrated for latitudinally different populations of *Fringilla coelebs*).

Whatever the contemporary significance of the photoperiodic responses of low-latitude and equatorial species may be, it is interesting to consider them in the light of possible "preadaptions" that could permit these populations, with further selection, to occupy higher latitudes, either permanently or as summer breeding populations, where precise photoperiodic controls may be necessary in timing the annual cycles with respect to much shorter suitable periods for reproduction.

As has Immelmann (1963) in a broader sense, Wolf (1969) concludes, specifically for *Zonotrichia capensis*, that it is more profitable to think of a series of proximate factors, rather than a single factor, "and very likely different ones in various populations. . . ." With this we are inclined to agree, although it seems more likely that populations differ in the relative emphases and the "interpretations" placed on individual proximate factors as environmental information rather than using "different" sources of information. Into such considerations must be injected the suggestions of Immelmann (1963) concerning endogenous (presuambly circennial) reproductive periodicities that become annual cycles because of *Zeitgeber* functions of proximate factors.

Clearly the skimpiness of our empirical knowledge of the details of the breeding cycles of low-latitude and equatorial species is surpassed only by our ignorance concerning the mechanisms that control these cycles. What is exciting now are the opportunities offered by the abundant, widespread populations of *Zonotrichia capensis* for combined laboratory and field studies of these mechanisms.

SUMMARY

A series of experiments under controlled conditions clearly demonstrates the existence of

photoperiodic testicular responses in *Zonotrichia capensis costaricensis.* This confirms earlier observations by Miller on an equatorial population in Colombia. A consideration of the natural breeding cycles of *costaricensis* leads to the tentative conclusion that photoperiodic mechanisms may have no more than a minor role, if any, in reproductive periodicity. However, a resolution of this question must await more extensive field investigations and laboratory experiments.

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