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MORPHOLOGICAL CHANGES IN THE THYMUS OF YOUNG AND ADULT RED-BILLED QUELEAS *QUELEA QUELEA* (AVES)

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CONTENTS

In a wild population of red-billed queleas *Quelea quelea* L. (Ploceidae: weaver-birds) sampled throughout the year in East Africa, the thymus was found to enlarge in young birds shortly after hatching, remain enlarged during the juvenile stage, and regress towards the end of the postjuvenile moult. In adults, recrudescence occurred in many individuals during the prenuptial and postnuptial moults, and also in most if not all individuals, of both sexes, for a brief period during a breeding session.

Thymus enlargement in both young and adults has been found to be accompanied by marked erythropoietic activity within the gland, and it is suggested that this activity is related to an increased demand for erythrocytes which may occur during moult and breeding.

Introduction

The thymus gland of birds and mammals is generally considered to reach maximum size in the developmental period before the attainment of sexual maturity, and thereafter to involute slowly with increasing age. However, most of the observations from which this generalization has been made relate to domestic or laboratory animals, whereas in the few studies on wild populations seasonal recrudescence of the thymus has been shown to occur regularly in normal healthy adults. Thus, Höhn (1947, 1956) found thymus enlargement

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following the breeding season in adult mallard ducks *Anas platyrhynchos*, American robins *Turdus migratorius* and house sparrows *Passer domesticus* in North America. Similar postbreeding thymus enlargement has also been noted in a tropical species, the yellow-vented bulbul *Pycnonotus goiavier*, studied in the climatically near-constant environment of Singapore (Ward & D'Cruz 1968). In this case it was postulated that the recrudescence was associated with the moult, the thymus being involved in the production of blood cells required when blood volume supposedly increases during the period of feather growth. Similarly, Anderson (1970) showed thymus enlargement during moult in the ring-necked pheasant *Phasianus colchicus* and tentatively suggested that extra lymphoid cells might be needed to aid survival, by enhancing immune responsiveness, through the moult when stress resistance may be low. Among wild animals, thymus enlargement in adults has been recorded in red-backed mice *Clethrionomys rutilus* in which it was correlated with increased reticulocyte numbers (Sealander & Bickerstaff 1967), and in female mule deer *Dama hemionus* (Browman & Sears 1956).

Many aspects of thymus function are still controversial, and while there seems to be little doubt that in young mammals it plays an important role in immunological response, its function in birds is not clear (see Payne 1971; Assenmacher 1973). The formation of erythrocytes in the thymus of the laboratory mouse has been reported by Albert, Wolf & Pryjma (1965), but large scale erythropoiesis has been found only recently in wild *Quelea quelea* (Kendall & Ward 1974).

In the present study, we have followed changes in the size of the thymus, with age and season, in wild red-billed queleas *Q. quelea*, small, mainly granivorous weaver-birds abundant throughout the semi-arid grasslands of tropical Africa.

Materials and methods

The data used in this study were obtained from over 5000 individuals collected in various localities in Tanzania and southern Kenya in the course of an ecological investigation of this important agricultural pest. All specimens belonged to the race *Q. q. intermedia* Van Someren, which may be regarded as a single population, the members of which move about constantly within a vast area of East Africa (Ward 1971). Samples were obtained in all months from 1969 to 1971, mostly by mist-netting in large communal roosts and breeding colonies.

All specimens were killed on capture. Routine examination included sexing and gonad measurement, determination of moult condition, and, in the case of first-year birds, ageing by reference to the degree of cranial pneumatization and moult. In females a further age criterion which proved useful once the cranium had become fully pneumatized was the shape of the oviduct: straight in first-year individuals and convoluted in older birds which had previously laid.

The moult condition was determined as follows: in the postnuptial moult of adults, and in the corresponding postjuvenile moult of young birds, both of which are 'complete' moults involving renewal of the entire plumage, the primary score method was used. Each of the nine primaries was scored as four when fully grown, and as three, two or one when three-quarters, half or quarter grown, to give a maximum score of 36 when the moult of all primaries is complete. Since primary moult takes about 3 months and virtually spans the moult of the whole plumage, and proceeds at a fairly constant rate, the primary score provides a good index of the progress of the postnuptial moult.

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The prenuptial moult, which is 'incomplete' involving only the small feathers of head and body, cannot be followed with similar precision. However, the males, which change from drab non-breeding plumage to a brightly coloured breeding dress, could be classified subjectively as being in early, mid-, or late moult; this could not be done with the females, which change from one drab plumage to another which is similar.

The thymus of *Q. quelea* consists of about a dozen distinct lobes arranged in two chains, one on each side of the neck. The thymus of each bird examined was classified as 'regressed' when the lobes were only 1 mm long or less, flat and white (and often difficult to find). 'Enlarged' thymi had the lobes greatly swollen, often more than 4 mm long, and pink in colour: frequently one or more of the lobes was red or had red patches showing that they were filled with red blood cells. 'Intermediate' thymi had lobes of intermediate size and only occasionally did they show red patches; glands which were enlarging could not be distinguished from those which were regressing. Young individuals often had thymi relatively larger than the enlarged lobes of adults and were designated as 'very enlarged'.

Changes in thymus size will be described for young birds according to their age. At about 6 months of age they complete the postjuvenile moult and become, by definition, (first-year) adults. For adults the thymus changes will be related to stages in the annual cycle, the main features of which are two moults, together occupying about 6 months (in this population the prenuptial moult starts as the postnuptial moult comes to an end), and an equal period when the birds are in breeding plumage. This latter period may be referred to as the breeding season, though this does not necessarily mean that all individuals are able to reproduce throughout the period. Queleas breed in very large, well synchronized colonies formed where a group of individuals ready to breed find a suitable locality. When a particular breeding session, lasting about 6 weeks, is over and the young have reached independence, the adults generally move away from the area – apparently in search of a new breeding locality (for details of the complex movements of queleas in East Africa, see Ward 1971).

Outside the breeding season, when thymus changes are being related to moult, all data gathered from samples collected over a wide area of East Africa (wherein the birds are constantly moving about) have been pooled. However, during the breeding season such pooling is not feasible since the rapid changes in thymus size are clearly related to the sequence of events during an actual breeding session. Accordingly, for this purpose the colonies sampled are treated separately. The percentages of birds with thymi in each category are shown in figures 1–4; actual numbers were used to compute the values of χ^2 from contingency tables. The probability of the occurrence of these χ^2 values has been given to indicate the degree of significance between points on the figures.

Results

Thymus changes in young

No significant differences between the sexes have been detected in thymus changes in young queleas, so data for males and females are considered together.

As figure 1 shows, embryos about to hatch had small thymic lobes. However, by the age of 10 days 28% had enlarged, and 52% intermediate (presumably enlarging) thymi, while at independence (age 3 weeks) 95% had enlarged or very enlarged thymi and none had them regressed.

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Of the 140 individuals collected in juvenile plumage (*ca.* 1–2 months old) 80% had enlarged thymi and in the course of the postjuvenile moult the proportion fell fairly steadily to reach 35% by its completion when the birds were about 6 months old. From then on, it was no longer possible to distinguish first-year males from older individuals with any certainty as the more precocious of them were attaining fully pneumatized skulls. First-year females remained distinguishable, however, on the basis of oviduct shape. Of the 287 first-year females collected while in their first prenuptial moult, 54 (19%) had the thymus enlarged and 111 (39%) had it regressed. Thus, the general decline in thymus activity in the population (in any individual, involution may have been rapid) apparently continued until at least the beginning of the birds' first breeding season. From results obtained in actual breeding colonies (see later) it seems likely that the thymus in most if not all first-year adults became regressed before they began their first breeding attempt.

Involution of the thymus with advancing maturity is, of course, quite unexceptional, being the general pattern found in all mammals and birds so far studied.

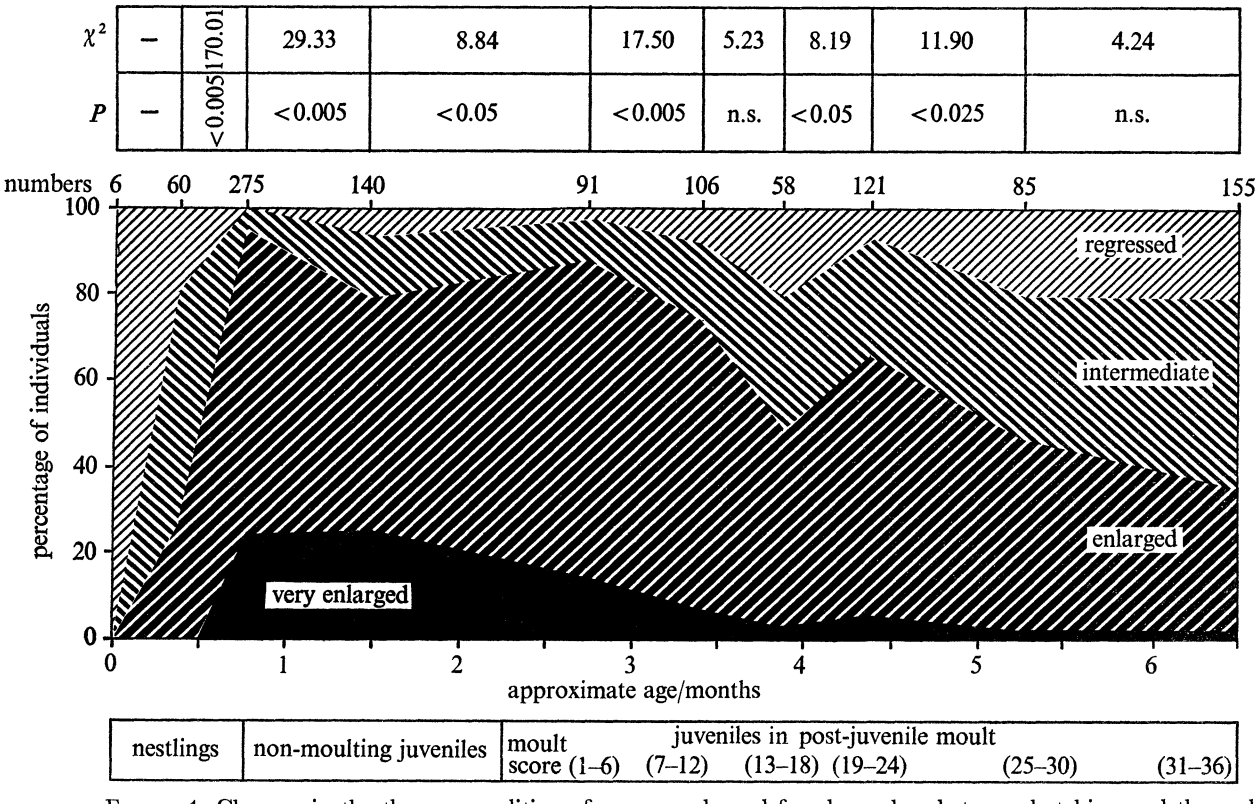

FIGURE 1. Changes in the thymus condition of young male and female queleas between hatching and the end of the postjuvenile moult. n.s., probability (*P*) greater than 0.1.

Thymus changes in adults

In this section we consider those adults the age of which could not be determined (definite first-year females in prenuptial moult have been dealt with above). Since wild living *Q. quelea* appear to have an average adult mortality of around 60% annually, in common with many small passerine species, it may be assumed that, of the adults collected during the breeding season and when in postnuptial moult, roughly half were only 1 year old, a quarter 2 years old, and a very small proportion over the age of 4 years.

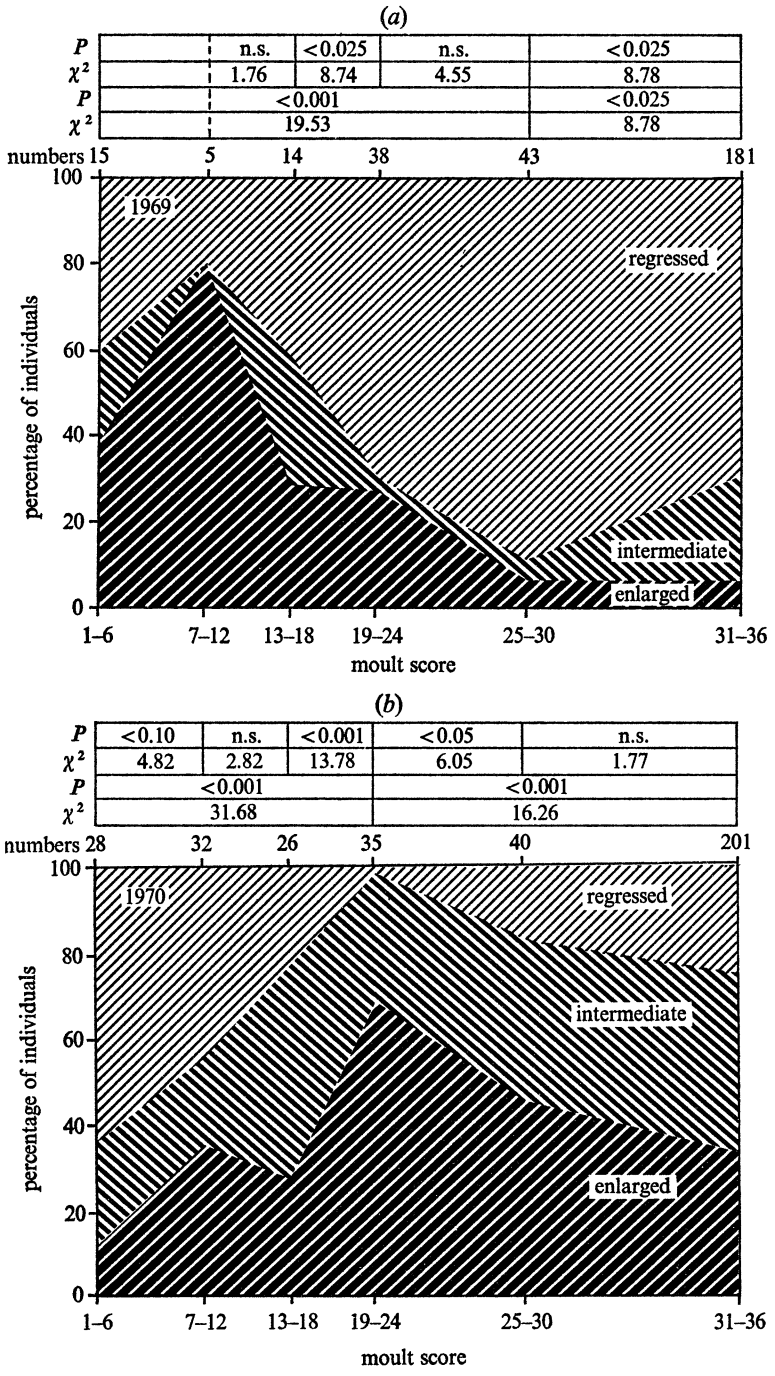

FIGURE 2. Relation between thymus condition and stage in postnuptial moult in adults collected in (a) 1969 (298 specimens), (*b*) 1970 (366 specimens). Note that the moult categories are spaced according to mean time interval. n.s., probability (*P*) greater than 0.1.

Postnuptial moult

Between 26 May and 24 October 1969, 298 adults at some stage in their postnuptial moult were examined. Between 60 and 80% of the birds had enlarged thymi at an early stage in the moult, but few thereafter (figure 2*a*). In contrast during 1970 when 366 moulting individuals were collected between 11 June and 26 October, peak enlargement of thymus corresponded with the later stages in the moult (figure 2*b*).

A very different picture was obtained from a group of adult females kept in captivity following capture in a breeding colony in Tanzania. These birds were kept in a large cage in Arusha, Tanzania and fed *ad libitum* on millet seed. At fortnightly intervals, five were taken at random and killed. Only one out of 35 birds killed during the postnuptial moult period had an enlarged thymus.

Prenuptial moult

Of 607 adult males (first-year and older) in prenuptial moult, collected mainly between September and December 1969 and 1970, only 109 (18%) had the thymus enlarged and in 269 (44%) it was regressed. No significant difference in thymus condition could be detected between males in early, mid- or late prenuptial moult, nor was there any correlation between thymus size and the size of the testes which were enlarging during the same period. Of 215 adult females (excluding first-year individuals) examined in 1969, only 7 (3%) had enlarged thymi and 167 (44%) had them regressed. In 1970 the proportions were similar, 7 (7%) of 97 females had enlarged thymi and 42 (43%) had them regressed.

Breeding season

The most complete record of thymus changes in adults engaged in breeding activities was obtained from a large, well synchronized colony (Makuyuni I) in northern Tanzania. The colony was first sampled on 3 February 1970 by which date it was 4 days old; most nests were already complete and many held the first of the 2–4 eggs which form a clutch. In only 10% of the males and 5% of the females was the thymus enlarged and in the great majority it was in the regressed state (figure 3). In the next two samples, collected on 5 and 7 February (corresponding roughly with the middle and end of egg laying in the colony), none of the males and only 5% of the females had an enlarged thymus. Following this period of low and apparently decreasing thymus activity there was a spectacular surge of activity which had already begun by 11 February when about 40% of individuals of both sexes had enlarged lobes. Over the next 2 weeks the proportion continued to increase, reaching a peak of 78% in males and 84% in females in the samples taken on 20 and 23 February respectively. The rapid rise in thymus size coincided with the incubation stage of the colony, the mean hatching date being 17 February. There was a great decrease in thymus size in many individuals between 23 and 26 February as shown in figure 3. At the end of the breeding session approximately 20% of males and 40% of females had enlarged thymi.

Three other colonies in the Makuyuni area, contemporaneous with the main study colony, but one to three weeks out of phase with it, and one of another race *Q. q. lathami* in Botswana, have also been sampled, though only in their later stages. In each case there was a decline in thymus activity after the end of the incubation period (figure 4) as in the main study colony.

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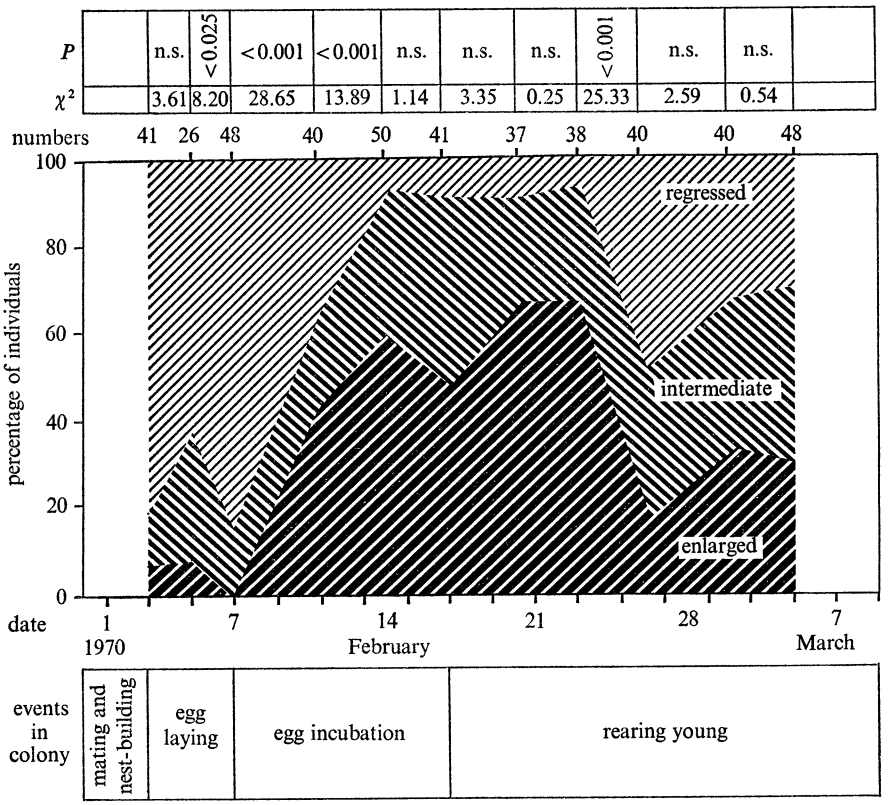

FIGURE 3. Thymus condition of adults (both sexes) breeding in the Makuyuni colony. n.s., probability (P) greater than 0.1.

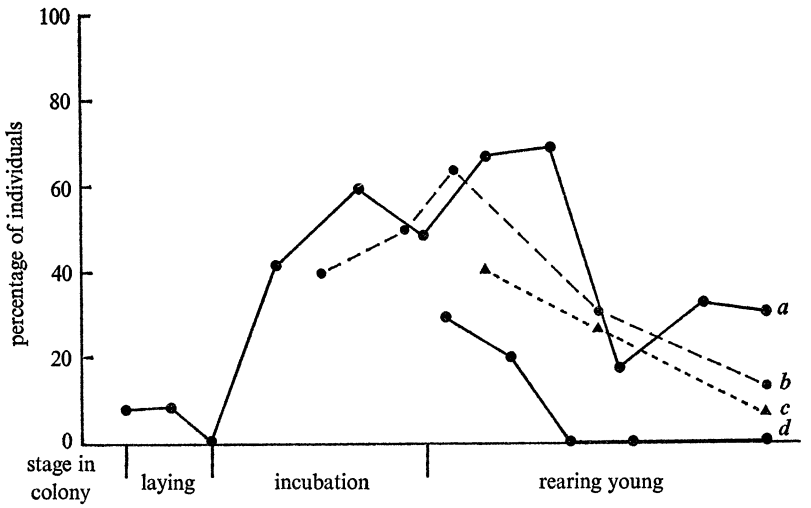

FIGURE 4. Percentage of individuals with enlarged thymus in samples of breeding adults taken at various stages in the life of four colonies: (*a*) The Makuyuni colony; (*b*) and (*c*) two other colonies in N. Tanzania; (*d*) colony of *Q. q. lathami* in Botswana.

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All the birds examined in the Makuyuni colony were subjected to carcass analysis for another study concerned with fat and protein changes in breeding adults (Jones & Ward, in press). As figure 5 indicates, the recrudescence of the thymus during the incubation period coincided with a rapid recovery in protein condition of the flight muscles, as indicated by the lean dry weight of the birds, which followed a fall to critically low levels during the first few days of the breeding session when the protein reserves are apparently drawn upon heavily owing to the demands of mating, nest-building and laying.

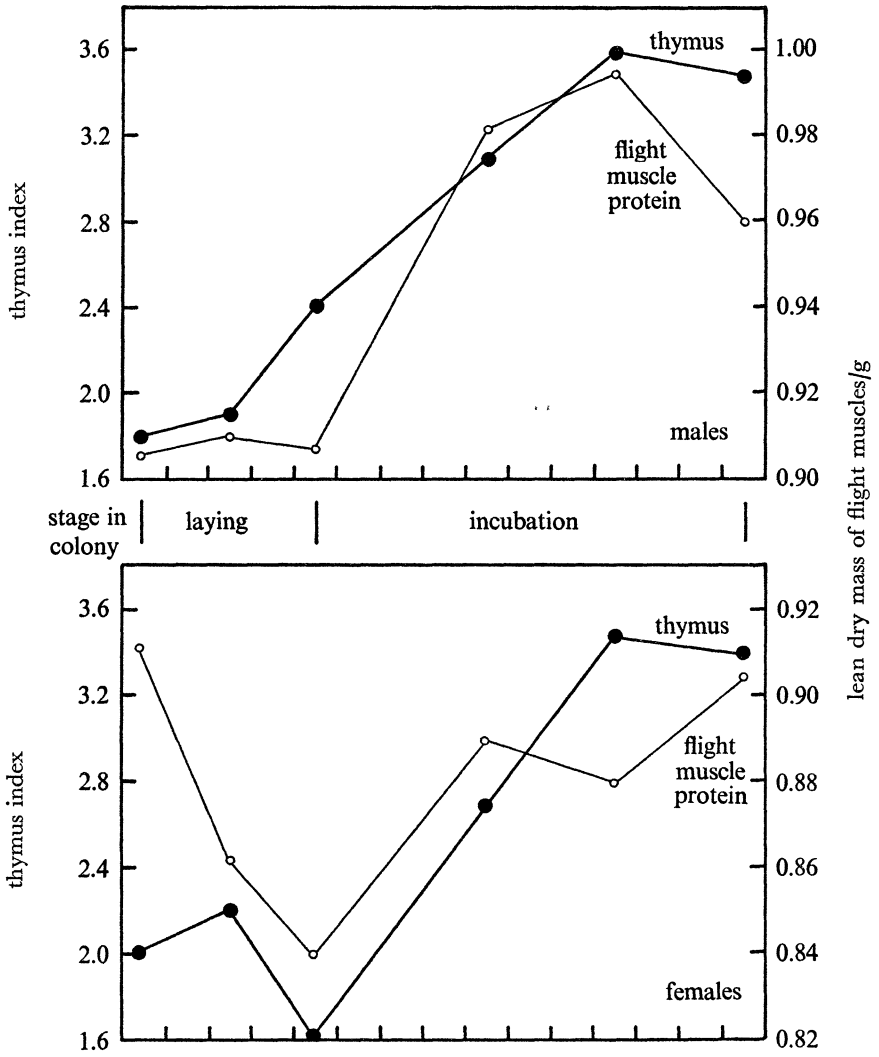

FIGURE 5. Comparison of changes in the thymus size and 'protein condition' of birds collected during the laying and incubation stages of the Makuyuni colony.

Note: the mean index of thymus size was obtained after scoring each individual's thymus as 4 when enlarged, 3 or 2 (depending on the size) when intermediate, and 1 when regressed. The protein condition is indicated by the mean mass of the flight muscles after removal of all lipids and water (data from Jones & Ward, in press).

DISCUSSION

In this study thymus changes have been followed by the examination of individuals sampled at random from the population. This method does not enable us to follow changes in any individual (except during the synchronized breeding sessions when extrapolation of data is

possible). Therefore our results do not preclude the possibility that in the course of a moult individual birds may experience several cycles of thymus enlargement and involution. At the other extreme it remains possible that some individuals may go through a moult without any thymus enlargement at all. Despite this failing in the method, there can be no doubt that the thymus is capable of enlargement in the adult at any time of the year. In a typical individual having two moults and breeding three times in the course of a breeding season, the thymus may well go through five or more cycles in a year. It seems logical to assume that each time the thymus enlarges it is performing some important function. Also, since the enlarged lobes in adult and young queleas have histological similarities (Bacchus & Kendall 1975), the function would be expected to be the same in sexually immature as in mature birds.

It has been customary to regard the thymus as part of the immunological apparatus, required by the immature animal but becoming permanently involuted when it matures. However, histological examination of the thymus in many of the specimens collected for the present study has suggested another hitherto largely unknown function, namely as an erythropoietic organ capable of producing large numbers of red blood cells (Kendall & Ward 1974). Large numbers of immature erythrocytes, together with lymphocyte-like cells, have been found in enlarged lobes from both breeding and moulting adults, as well as from young birds. We believe therefore that the thymus is probably erythropoietic whenever it enlarges. It is not yet clear, however, whether the erythropoiesis is in anticipation of an increased demand for red blood cells, or in response to anaemia.

We speculate that the young bird, which grows extremely fast to reach adult dimensions and body mass before it is 1 month old, may for this growth require a greater supply of erythrocytes than can be produced by the erythropoietic tissues (i.e. bone marrow, etc.). Moreover, it seems likely that the demand remains high throughout the postjuvenile moult, thus accounting for the large, though gradually diminishing, percentage of juveniles found to have enlarged thymi during the moult. Although there is no direct evidence that the blood volume, or total number of erythrocytes, increases during moult, such an increase seems likely in view of the increased vascularization of the feather follicle and the large amount of blood in the shafts of growing feathers. Rawles (1960) has stated that 'moulting imposes a severe strain on the bird's vitality because of the tremendous supply of blood necessary for the growth of new feathers, the number of which runs into thousands'.

The considerable percentage of adult individuals found to have enlarged thymi at some stage in the postnuptial moult (a complete body moult) and the smaller incidence during the prenuptial moult (which is a light moult) is also explicable in terms of the need for extra blood. The fact that thymus enlargement does not seem to be the prerequisite of any particular stage in moult, and may not occur at all in captive birds, suggests that some environmental factor such as food supply may be deciding the need for thymic erythropoiesis.

The thymus enlargement noted in breeding adults, which does not appear to have been noted previously in any bird species, coincides with a general recovery of protein and fat condition of the flight muscles previously lowered by the physiological demands made on the birds during the first few days of a breeding attempt. During this general recovery period it is quite possible that an extra source of red blood cells is required, either to help rectify an anaemia accompanying the fall in fat and protein reserves, or to speed recovery.

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