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Environmental and hormonal control of vernal migration in redheaded bunting (*Emberiza bruniceps*)

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Abstract. This paper reviews the factors and mechanisms which result in the development of the metabolic state characteristic of migration with special reference to a palaeotropical migrant the redheaded bunting, *Emberiza bruniceps*. Changes in climatic conditions and food supply act as proximate triggers of migratory behaviour in partial migrants. Typical migrants like buntings use daylength as a cue but the exact mechanism of how photoperiodic information is translated in terms of migratory events is still not known. Almost entirely the photoperiodic effects have been explained on the basis of the involvement of hypothalamo/hypophyseal system. We feel mechanism(s) other than those acting through neuroendocrine system may be equally important. Furthermore the role of temperature has not been adequately explored so far. Our observations indicate the possibility that redheaded buntings might integrate the information received from photoperiod with environmental temperature (and other factors?) resulting in the development of migratory state. The physiological control of avian migration is much less understood. Majority of papers have centered around the 'gonadal hypothesis' of Rowan supporting or contradicting it without providing conclusive evidence. Pituitary prolactin has also been shown to be implicated although the mechanism of action is only speculative.

Conclusive evidence for the involvement of thyroid hormones (thyroxine, T₄; triiodothyronine, T₃) in the physiological timing of migration has been produced attributing independent roles to T₄ and T₃. It is suggested that seasonal variation in peripheral conversion of T₄ to T₃ could serve as an effective strategy to render available the required thyroid hormones T₄ and/or T₃ during different phases of the year thus accounting for the metabolic switch over from T₄-dependent moult to T₃-dependent migratory fat deposition and zugunruhe and also ensuring preclusion of simultaneous occurrence of these mutually incompatible events. Considering that the number of environmental and physiological factors influence this mechanism and considering that thyroid hormone molecule has been put to a wide range of usage during the course of evolution the mechanism(s) of peripheral conversion of T₄-T₃ may assume great flexibility and have selective value-especially in migration which is known to have evolved several times in diverse avian families.

The attractiveness of this hypothesis lies in the fact that it has potential to explain the both physiological development of the metabolic state of migration and at the same time the physiological timing of migration not only with respect to the cycle of environment but also with respect to other conflicting seasonal events (moult and reproduction).

Keywords. Peripheral conversion; T₄-T₃; fat deposition; zugunruhe; thyroid; redheaded bunting.

1. Introduction

Migration in birds is a behaviour known to mankind since Vedic times (Atharveda 3000 BC; Jeremiah 8 : 7 Bible, Kalidasa 6th century AD) and is an adaptive response to what might be considered extreme environmental conditions. It involves

precise orientation and directed movements of a population over long distances. Migrations in many birds occur twice annually and are closely timed in accordance with ambient conditions. A northward journey to the breeding quarters occurs in spring and a southward migration to wintering grounds in autumn. The spring migration has been shown in many long distance migrants to be much faster as compared to the rather slow post-breeding movements to the winter quarters which involve a large proportion of juveniles (Berthold 1986). Over the course of a migration a bird encounters a variety of challenging habitats most of them with associated new food, new competitors and new predators. Crossing ecological barriers such as large bodies of water, deserts imposes special burdens on the energy and water budget of migratory birds. Energy needs during migration may be at least double the normal and bring many passerine species to the limits of their energy-acquisition ability (Berthold 1975; Perrins and Birkhead 1983). The success of migration would, therefore, depend on (i) how effectively a bird 'offsets' these costs of displacement and (ii) how well it times the movement with respect to the annual fluctuations in the environment. The migration period of passerines is characterized by two distinct phases (i) the premigratory preparatory period during which birds lay down enormous fat depots as energy reserves for flight accompanied by the development of a characteristic nocturnal restlessness known as 'zugunruhe' and the physiology of which is not understood and (ii) the endurance flight during which displacement takes place. While voluminous literature exists on the phenomenon of migration and its varied aspects our understanding of the control of this behaviour is still limited. It is however known that a number of migratory traits are genetically controlled which is not surprising considering the importance of migration in the life of a bird (Berthold 1975). In this paper through information available for a Palaetropic model, the redheaded bunting, *Emberiza bruniceps*, we explore the possible factors and mechanism(s) which result in the development of the metabolic state characteristic of migration.

Redheaded bunting is a passerine migrant belonging to the family Emberizidae, (*E. bruniceps*). It arrives in India in September and departs between March and early May for the breeding grounds in northern Baluchistan (Kalat, Quetta, Ziarat) in Palearctic zone (Ali and Ripley 1983; figure 1). Information on the exact times of yearly arrivals and departures is, however, lacking. Although it is distributed quite widely in the tropical winter quarters (8°N to 30°N) almost no studies have been carried out on its habitat ecology, potential competitors, diet and foraging behaviour. A characteristic premigratory disposition is elicited by excessive fattening and nocturnal restlessness (zugunruhe) which occur in caged birds also. Fat is deposited within 3–4 weeks in spring (30°N) preceded by significant hyperphagia. Zugunruhe also develops around the same time. Gonads develop in late spring and birds shows a strong postnuptial moult in August/September.

2. Environmental control of spring migration

Various environmental factors like photoperiod, temperature, food, wind direction, flying conditions, ice or snow cover, habitat destruction and other ecological factors are known to influence migration in birds. There are two ways in which environmental factors can exercise their influence (Baker 1938; Lack 1954) on bird migration.

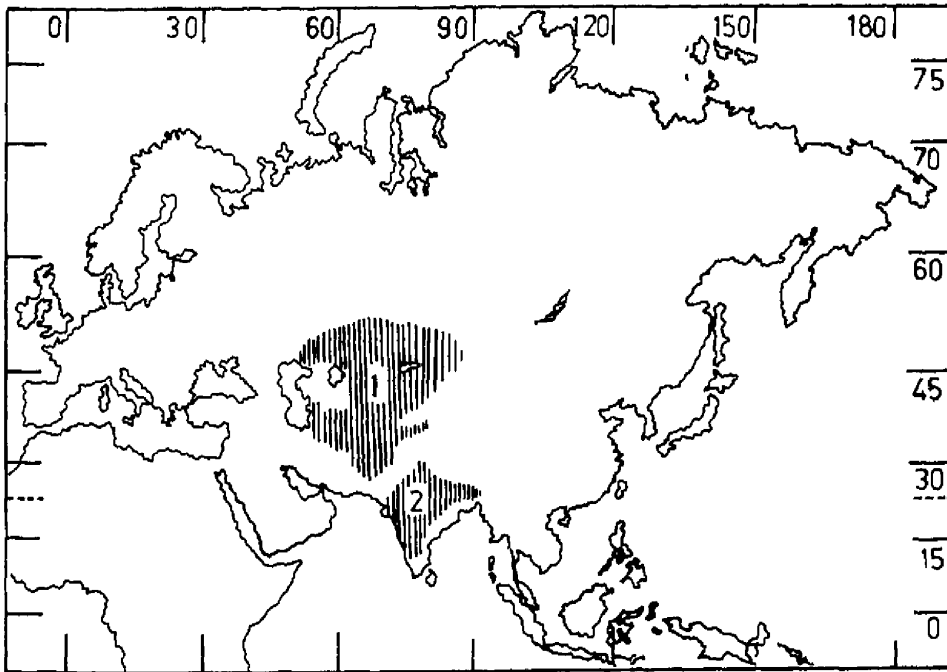


Figure 1. Distributional range of redheaded bunting *E. bruniceps*. 1, breeding ground; 2, wintering ground.

By affecting the evolution of a particular characteristic, in this case the timing of migration. The individuals that migrate at the best time are those most likely to survive. Factors that give survival value to the adaptation of the bird's cycle to that of the environment (termed ultimate factors) would be selected by nature during the course of evolution. However, in order to migrate at the right time physiological preparations for migration must commence much in advance of the actual departure. Any abiotic or biotic factor in the environment (termed proximate factor) could serve as a stimulus to initiate the migratory process—in this case the onset of fat deposition and zugunruhe. While changes in climatic conditions and food supply act as proximate factors to trigger migratory behaviour in partial migrants (e.g. European blackbird) they have little effect on typical migrants (e.g. willow warbler) (Berthold 1975). Plenty of literature exists to show that photoperiod provides the proximate stimulus for the onset of vernal migration (Rowan 1925, see for references Berthold 1975). Considering that adequate timing is crucial for successful migration the environmental cues used for triggering the onset of migration must be reliable and must have a predictive value. Photoperiod is perhaps the only environmental variable which meets both the requirements. Hence the widespread use of this factor for timing seasonal events in animal and plant kingdom. The physiological transduction of photoperiodic effects involves the hypothalamo-hypophyseal system and a phase of photoinducibility which is controlled by circadian system (Hamner and Enright 1967; Farner 1950). But how exactly the photoperiodic message is eventually translated in terms of migratory events is far from clear. Photoperiodic information may be of limited value in birds which breeding in temperate zones migrate to equatorial regions for winter, and, which despite the

insignificant photoperiodic changes on the equator, depart very precisely at the appropriate time for their homeward migration. Use of endogenous mechanisms (Miller 1965; Marshall 1960) like circannual clocks (Gwinner 1972, 1977) for the timing of vernal migration has been suggested in these birds. Because of their quasi-annual nature circannual clocks eventually require some environmental information to be synchronized with the calendar year. That photoperiod acts as a synchronizer of circannual rhythms of migration and reproduction is well established (Gwinner 1981; Berthold 1974, Chandola *et al* 1983; Bhatt *et al* 1986). However, physiological basis of the circannual clock and its interaction with the photoperiod is not at all understood.

Artificially simulated long days induce zugunruhe and excessive fat deposition in redheaded bunting (30°N) where as birds on artificial winter daylengths neither show zugunruhe nor fatten (Nair N G, unpublished). In the related migratory species blackheaded bunting (*E. melanocephala*) also significant fattening occurs with artificial photostimulation (Tewari and Kumar 1983; Kumar 1988; Devi and Lal 1992). Obviously variations in daylength provide the necessary environmental cue for triggering the spring migratory events in these buntings. Photoperiodic time measurement through circadian components has also been demonstrated in the response (Tewari *et al* 1982). It is, however, not known whether daylength acts directly as a 'driver' (as in baya weaver for reproduction, Chandola *et al* 1983) or as a 'synchronizer' (as in spotted munia, *Lonchura punctulata*, Chandola *et al* 1983). An interesting observation is that the onset of migratory behaviour in caged buntings held in ambient conditions at 30° N in the year 1991 and 1992 (Choudhary and Chandola-Saklani, unpublished) indicated a significantly earlier onset in 1992. Considering that the seasonal rise in temperature also occurred earlier that year these preliminary observations argue for a role of temperature. Nakamura and Kitahara (1983) too have made similar observations. The interaction of photoperiod and temperature, therefore, needs to be reassessed in the present context. It is quite likely that the increasing daylength of spring prepares the birds physiologically bringing them into a "ready state" from where they can migrate as soon as appropriate temperature is reached. Such integration of environmental cues has been shown in tropical birds e.g. of photoperiod and rainfall in baya weaver (Chandola-Saklani *et al* 1990). The remigratory fat deposition in *E. bruniceps* like in many other passerines, is preceded by hyperphagia and restricted diet inhibits development of zugunruhe and fattening (B K Choudhary, personal communication). The effect of photoperiod on food consumption may be *via* neuroendocrine axis and/or may involve peripheral mechanisms. This is another area open to investigation.

3. Physiological control of spring migration

The migratory period of passerines includes two important physiological mechanisms (i) the rapid deposition of large amounts of fat during premigratory preparatory period when migratory disposition develops and (ii) the utilization of these fat stores during the endurance flight which may metabolically be regarded as a very rapid starvation process (Jenni and Jenni-Eirmann 1994). Fat deposition is the most economic physiological strategy to cope with long migratory flights since fat provides more energy per gram than either protein or carbohydrate. In addition,

water is produced as fat is burnt thus preventing birds from becoming dehydrated (Phillips *et al* 1985).

While considerable investigations have been carried out to understand the process of lipid metabolism and avian energetics during migratory period very little is known of its control. The physiology of zugunruhe remains to be understood.

Hormones have been implicated in the onset of vernal migration. Rowan (1931) first proposed that spring migration is stimulated by hormones secreted by developing gonads under the influence of long days. These results were partly confirmed by Wolfson (1942) in other junco races. Several other workers also suggested that sex hormones play a stimulatory or atleast a modifying role in bird migration (Farner 1955; Berthold 1971). Recently, testosterone was shown to delay the termination of vernal migratory behaviour in captivity (Schwabl and Farner 1989). On the other hand, castrates of several migratory species display migratory behaviour (Putzig 1937; Farner 1950). For instance in blackheaded buntings *E. melanocephala* vernal zugunruhe in intact as well as castrated birds occurs almost at the same times (Jain N and Kumar V, personal communication). Hemicastrated and castrated redheaded buntings also fatten as much as intact birds when exposed to long days (Kumar and Kumar 1990). Thapliyal and Singh (1979) reported occurrence of unrestricted fat deposition in castrated redheaded buntings although gonadal hormones seem to influence free fatty acid and cholesterol metabolism. Similar responses have been reported in *Zonotrichia atricapilla* (Morton and Mewaldt 1962) and *Fringilla montifringilia* (Lofts and Marshall 1961). An interesting finding is that castration in several species (e.g. white-throated sparrow, buntings) may abolish photo-induced fattening and zugunruhe but only if the testes are removed *before* but not *after* the onset of photostimulation. This may explain the discrepant responses observed in literature and also rules out a primary regulatory role for androgens which however may be required only in very early stages of initiation of migratory disposition perhaps through complex interactions with other hormones. It is known that even the testes of sexually quiescent birds secrete minimal amounts of androgens and it is quite possible that androgens bring about a change in the sensitivity of higher photoresponding mechanisms (photoreceptors?) towards environmental photoperiod. This has actually been demonstrated for the onset of photorefractoriness in the reproductive cycle of baya weaver (Nair 1994).

Among other hormones prolactin (PR) has been implicated in migration. Administration of this pituitary hormone was shown to induce fat deposition and zugunruhe (Meier and Ferrel 1978). This observation is consistent with the finding that concentration of pituitary prolactin are at their highest during migration. PR stimulates fat deposition in redheaded bunting also most likely through hyperphagia (unpublished personal data). Corticosterone was also shown to augment migratory disposition to a certain extent (Ramenofsky *et al* 1992).

Detailed investigations from our laboratory have provided unequivocal evidence that thyroid hormones, thyroxine (T4) and triiodothyronine (T3) play an indispensable role in the development of vernal premigratory disposition.

4. Thyroid hormones

Considering the well known effects of thyroid hormones on both lipogenesis and

lipolysis (Pitt-Rivers and Tata 1959), processes central to migratory physiology, there have been attempts earlier to correlate seasonal thyroid activity with migration but data were limited to histological parameters only, no detailed biochemical studies having been undertaken (Putzig 1937; Oakeson and Lilley 1960; Wilson and Farner 1960; George and Naik 1964). Attempts have also been made implicating thyroid hormones in the locomotor activity and fat stores of migratory birds (Wagner 1930; Merkel 1938, 1960; Schildmacher and Rautenberg 1952, see rev. Farner 1950; John and George 1967) but considering the small number of birds involved and the variability of results even with similar doses of hormones the investigation reports can only be suggestive. In redheaded buntings *E. bruniceps* detailed studies were undertaken to assess the exact role of thyroid hormones in the development of vernal migratory behaviour. Three different approaches were taken *viz.*, seasonal thyroid hormone profile in relation with migratory disposition in wild caught and captive birds, effects of thyroid extirpation and hormone replacement therapy on migratory events and effects of suppression of peripheral monodeiodination of thyroxine on development of migratory disposition.

4.1 *Seasonal thyroid hormone profiles in relation to migration*

As in other vertebrates, T4 and T3 are the two prevalent circulating thyroid hormones in migratory passerines. T3, a major portion of which has been shown to be derived from monodeiodination of T4 is supposed to be the finally active form (Ingbar 1985). Our studies with non mammalian vertebrates including buntings have challenged this prevailing concept attributing an independent hormonal role to T4.

The first systematic seasonal study on thyroid hormone profiles in any passerine bird was performed by Pathak and Chandola (1982a) in buntings. A significant decline in plasma T4 concentration with two to three-fold increase in circulating T3 and T3/T4 ratio from January to February was observed (figure 2) which was subsequently found to be due to enhanced peripheral conversion of T4 to T3 (Pathak and Chandola 1982b). The increased plasma T3/T4 ratio thus precedes the remigratory disposition. This elevation in circulating T3/T4 ratio was registered only during spring premigratory period no significant changes in circulating thyroid hormones occurring during autumn migratory period. It is significant that no fat deposition occurs either in these buntings held on their wintering grounds during autumn migration. Perhaps different (thyroidal) mechanisms may be involved in spring and autumn migratory periods during which birds have been shown to behave quite differently (Berthold 1986). Recently, Ramenofsky *et al* (1992) studying the foraging ecology, hormonal and metabolic aspects of migration in dark eyed juncos *Junco hyemalis* also suggested the possibility of diverse mechanisms for spring and autumn migration.

4.2 *Thyroidectomy and hormone replacement therapy*

Thyroidectomy during vernal migratory period completely abolished premigratory zugunruhe and fat deposition. Effects of thyroidectomy on both parameters were restored with the administration of either T4 or T3 (figure 3), the response being linear (Pant and Chandola-Saklani 1993). This is the first consistent report of the

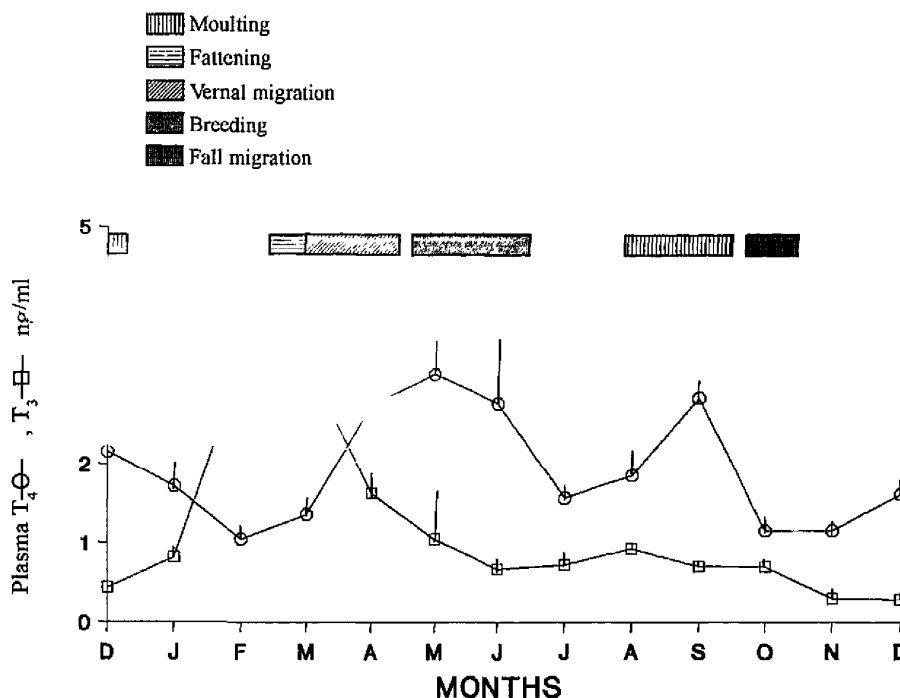


Figure 2. Circulating thyroid hormone profile and the seasonal physiological events in a captive population of redheaded bunting. The fattening role of thyroid gland is reflected by T3 levels and the progonadal and moult stimulatory role by T4. In this bird fat deposition occurs only during spring and not during autumn migration. Note the failure of T3 to rise before autumn migration.

involvement of thyroid hormones in the development of zugunruhe in any migratory bird. Earlier, Pathak and Chandola (1982b) demonstrated in bunting that thyroid ablation prevented fat deposition and replacement therapy partially restored the loss but findings were based on single hormone dose administration. Fat deposition was also reported to increase following small doses of thyroxine injection (Scildmadacher and Rautenberg 1952) and Merkel (1958) reported inhibition of migratory restlessness in methylthiouracil (an inhibitor of thyroid hormone synthesis) treated birds. However, reproducible results were not obtained (Merkel 1960; Wilson and Farner 1960).

4.3 Effect of suppression of extrathyroidal conversion of T4 to T3 on vernal migratory disposition

Considering the effects of thyroidectomy (Tx) and replacement therapy in buntings and the observed premigratory rise in circulating T3 it appears that T3 is more importantly involved than T4 in the development of vernal premigratory disposition. To test this possibility effects of suppression of peripheral monodeiodination of T4 were studied with a widely used inhibitor, iopanoic acid (IOP) (Pant and Chandola-Saklani 1993). Blockage by IOP, of extrathyroidal conversion of exogenous

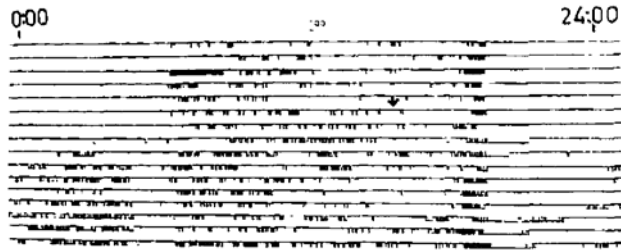


Figure 3. Perch hopping activity rhythm of thyroidectomized redheaded bunting during the premigratory period. An actograph of a single bird is reproduced, although actograms for 8-10 birds were recorded throughout the experiment. Note the resumption of nocturnal restlessness after administration of $1 \mu\text{g T}_3/\text{day}$ (\rightarrow).

T4 to T3 in Tx birds was found to prevent normal fat deposition during premigratory period. This clearly indicates that the lipogenic effects of T4 during vernal premigratory period are brought about through its monodeiodination to T3. Similarly, when conversion of endogenous T4 to T3 was blocked in intact birds zugunruhe as well as fat deposition was completely inhibited (figure 4). In other words, behaviour of inhibitor treated birds and Tx birds was similar. This argues for a distinct role of T3 in the expression of zugunruhe like that of fat deposition. However, in the same birds, unlike the effects of T4-induced fattening and zugunruhe, IOP-blockage of monodeiodination of T4 did not result in the suppression of T4-induced feather regeneration. To the contrary IOP further stimulated feather regeneration and growth in a dose dependent manner in Tx birds receiving T4. It is clear that T4 effect on feather regeneration and moult as in another passerine (spotted munia, Pant and Chandola-Saklani 1992) does not involve prior conversion to T3 attributing an independent hormonal role to T4. This is contrary to the prevailing concept. General consensus holds that T4 is a prohormone T3 its

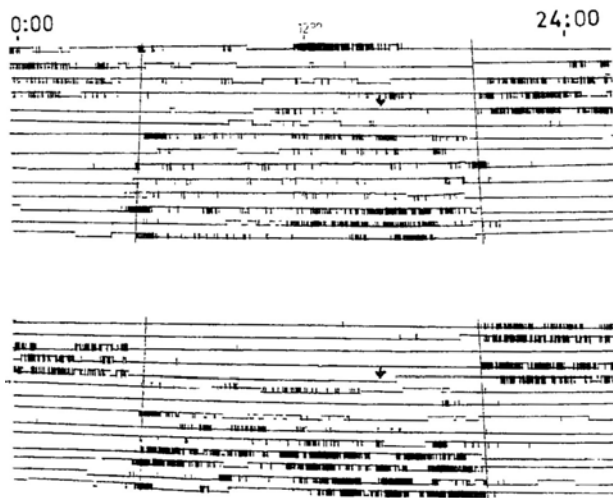


Figure 4. Two intact redheaded buntings receiving 1.5 mg of iopanoic acid per day over 10 days. Note the disappearance of zugunruhe. The arrows indicate the time and day of daily injections.

monodeiodinated derivative being the finally active compound (Ingbar 1985). Effects on migratory disposition in buntings indeed conform to this view point but our results show that T4 effects on reproduction (Pant and Chandola-Saklani 1993) and moult (Pant and Chandola-Saklani 1993) in birds, as in lizards, are not mediated *via* its conversion to T3 (Chandola-Saklani and Kar 1990). Obviously both T4 and T3 appear to have specific roles arguing for a hormonal role for T4. This may have significant implications in the physiological timing of the seasonal events which must occur within the given annual span.

5. Physiological timing of migration and other seasonal events: A role for peripheral monodeiodination

A prerequisite in the life of a migratory bird is the adequate partitioning of conflicting energy demands with other seasonal events. Physiological events having high energy and nutritional requirements like migration, moulting, and reproduction, therefore, can not occur simultaneously and must be temporally spaced according to the seasonally changing demands of the environment. But not much is known about how this is achieved. In buntings as in many other birds all these events i.e. migratory disposition (fattening and *zugunruhe*), moult and breeding are temporally spaced and have been shown to be influenced by thyroid status (Pant and Chandola-Saklani 1993; Devi and Lal 1993). Also in other birds which have been studied the thyroid seems to be associated with atleast one or two, if not all, of these physiological events (Assenmacher and Jallageas 1980; Voitkewitsch 1940; Thapliyal 1969; Chaturvedi and Thapliyal 1979; Lal and Thapliyal 1982; Wilson 1994; Follett *et al* 1988).

Thyroidal extirpation in buntings leads not only to the suppression of premigratory disposition but that of gonadal growth and feather regeneration also, and, replacement therapy restores all the effects on all three physiological events. Clearly, the thyroid gland has a progonadal, moult-stimulatory and fattening role in this bird. In experiments described above it was shown that the effects of thyroid hormone on fat deposition and *zugunruhe* during premigratory period are brought about by T3 while those on moulting and feather regeneration directly by T4 (Pant and Chandola-Saklani 1993). In the circulating hormonal profiles the progonadal relationship is reflected by T4 while the vernal premigratory events coincide with high levels of T3. These seasonal variation in circulating T4 and T3 have been shown to be due to variations in peripheral conversion of T4 into T3. Obviously, seasonal variation in peripheral conversion of T4 could serve as an effective strategy to render available the required thyroid hormone, T4 and/or T3 selectively during different phases of the year-thus accounting for the metabolic switch over from T4-dependent moult to T3-dependent migratory fat deposition and *zugunruhe* and also ensuring preclusion of simultaneous occurrence of mutually incompatible events. The effect of T3 on fat deposition may be direct on the process of lipogenesis in the liver or indirectly through food intake (figure 5). The former possibility is more likely. The mechanisms involved in the response of *zugunruhe* to T3 are not known but may involve neural effects.

Thyroid, alone by itself, can not be the physiological trigger for migratory disposition. What are the environmental cues and how are they translated in terms of thyroid

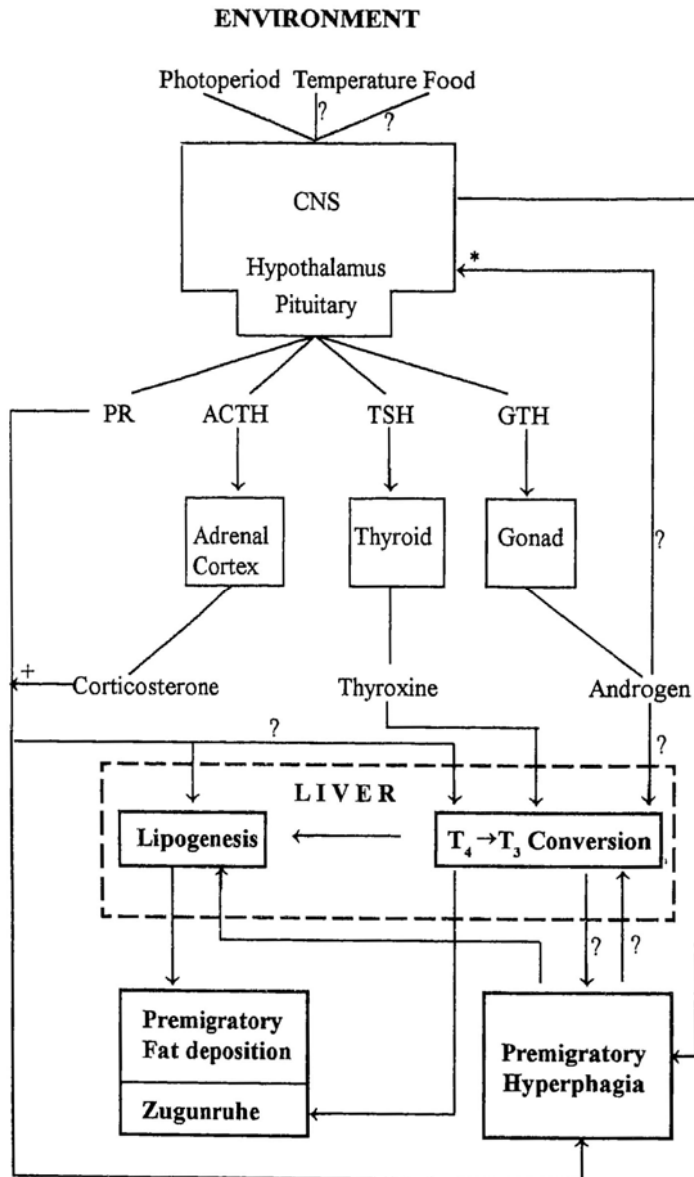


Figure 5. Possible factors and mechanism(s) involved in the control of the development of migratory disposition in spring. Question marks show speculated pathways. +, Corticosterone is synergistic with PR; *, Androgens could also act on the higher photorepsonding mechanisms modulating response to photoperiod. CNS, Central nervous system; PR, prolactin; ACTH, adrenocorticotrophic hormone; TSH, thyroid stimulating hormone; GTH, gonadotropic hormone; T₄, thyroxine; T₃, tri-iodothyronine.

hormone metabolism? One possibility is through the mediation of neuroendocrine system. Photoperiod and temperature both have been shown to act on the hypothalamo/hypophyseal/thyroid axis bringing about changes in general metabolism. While temperature effects on thyroid are well documented, photoperiod has been shown

in a number of birds like Japanese quail, ducks, fowl and poultry to stimulate thyroid function (see for references Wentworth and Ringer 1986). In redheaded buntings artificial photostimulation enhanced monodeiodination of T4 (Pant and Chandola-Saklani 1993) but these results need to be further confirmed with other rigorous approaches. Also pituitary prolactin is known to influence thyroid functions (figure 5).

It appears to us that the investigations on photoperiodic responses in vertebrates have overly emphasized the role of hypothalamo/hypophyseal complex ignoring almost entirely the general effects of photoperiod not necessarily mediated *via* neuroendocrine system. Effects of environmental factors, including photoperiod, produced through mechanisms other than those involving the neuroendocrine system may be equally important, e.g. an effect of enhanced food intake on T4-T3 metabolism resulting from photo-induced hyperphagic behaviour. In spotted munia artificial food restriction influences thyroid metabolism (Chandola and Pathak 1980) and in rat and eels T4-T3 conversion specifically (Ingbar and Gallon 1975; Chopra 1981; Higgs and Eales 1977). Equally possible is an effect of change in the quality of food available on the environment during spring. In rats T3 production is altered depending on whether fed by a carbohydrate or protein-rich diet (Chopra 1981). No data are available in the actual diet of redheaded bunting but an arthropod abundance, and hence availability of protein-rich food, in spring is a normal phenomenon reported in their tropical winter quarters (Sharma 1987). Experiments to test these possibilities are in progress.

It is obvious from the above review that thyroid hormone(s) (T3) plays more than a permissive role in the control of development of migratory disposition—the peripheral conversion of T4 → T3 being the important regulatory step. The fact that a number of environmental and physiological factors influence this mechanism and the wide range of usage of thyroid hormone molecule during the course of evolution lend to it a great flexibility and hence selective value—especially in migration which is known to have evolved several times in diverse avian families.

The attractiveness of this hypothesis lies in the fact that it has the potential to explain both physiological development of the metabolic state of migration and at the same time the physiological timing of migration not only with respect to the cycle of environment but also with respect to other conflicting physiological events (moult and reproduction).

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