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Annual migration: Strategy for twice-a-year long-distance travel in obligate latitudinal nocturnal avian migrants

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Abstract

Latitudinal avian migrants show comprehensive changes at multiple levels in response to the prevailing environmental conditions, for example, photoperiod, temperature and food availability. These changes aid in decisions when birds begin their migratory flights. Twice-a-year, changes in identifiable, distinct behavioral and physiological phenotypes favor the generation and overall flux of energy required for the nocturnal migratory flight. For example, the accumulated fat stores *via* free fatty acids oxidation in the liver and protein-mediated transport supply energy required by the 'working' (flight) muscles while birds are in migration flight. However, it is still poorly understood how latitudinal migratory species prepare differentially for two similar seasonal travels; southwards in autumn to escape from the harsh winter condition at breeding grounds, and northwards in spring to reproduce. In this brief article, we aim to provide insights into seasonal plasticities that allow an obligate latitudinal migrant to accomplish annual journeys between nearly fixed destinations, based mainly on research in our laboratories on Palaearctic-Indian migratory buntings over the last four decades.

Keywords: Bunting, *Emberiza bruniceps*, *Emberiza melanocephala*, Migrant behaviour, Migrant physiology, Photoperiod response

Introduction

The annual itinerary of a typical avian migrant includes mainly six seasonal life history states (LHSs), namely reproduction, post-breeding moult, autumn migration, wintering, pre-breeding moult (may be sparse or absent in some species), and spring (vernal) migration. Thus, with the migration taking place before and after reproduction, millions of songbirds follow more rigid annual schedules. All seasonal LHSs are identifiable by drastic changes in behavior and physiology as required to begin and end a successful journey of several hundred kilometers. Most important changes are linked with the timely departure of birds to allow them to explore, in particular, feeding resources at the wintering ground, and nesting resources at the breeding grounds in order to enhance the reproductive success (Ramenofsky & Wingfield, 2007; Kumar *et al.*, 2022, 2025; Helm & Liedvogel, 2024).

Regular variations in environmental agents synchronize, if not drive, changes in behavior and physiology to occur at the most profitable time of the year. For example, when the breeding season ends, migrants prepare for their southward travel to the wintering area in response to the post-equinox decreasing autumn (≤12 h) photoperiods, which can still be close to the threshold for photoperiodic induction in spring. Conversely, the overwintering migrants begin to prepare for their northward travel in response to post-equinox increasing spring (≥12 h) photoperiods. The ambient temperature also seems to play a crucial role in the developing the migration phenologies (Singh *et al.*, 2012; Sur *et al.*, 2020). Therefore, the migratory departure decision is the outcome of integrating changes in photoperiod and temperature, along with food availability, that regulates behavioral and physiological phenotypes associated with migration (Kumar *et al.*, 2025).

In this article, we aim to highlight adaptive strategies that migrants employ between non-migratory and migratory, as well as between spring and autumn migratory LHSs. The discussion is based on experimental evidence, mainly from laboratory research carried out in our laboratories over more than four decades using two migratory species, the black-headed bunting (*Emberiza melanocephala*) and red-headed bunting (*Emberiza bruniceps*). These species measure about 16-18 cm in length, although black-headed bunting is relatively larger. The two buntings are sister species and partially overlap their breeding and wintering areas. Both are obligate latitudinal migrants, and follow a predictable annual to-and-fro migration between breeding sites (~40° N in west Asia and southeast Europe, including Indo-European flyway) and wintering sites spread mainly over a large part of central and north India, 20-27°N (Ali & Ripley 1999; Ćiković *et al.* 2021). Further, they represent the Palearctic-Indian migration system, which is the least studied of the major migratory systems of the world (Galbraith *et al.*, 2014). In late September/ October, both bunting species arrive in India. After an overwintering period for about six months, they begin to return very late in March or early April when the natural light period (sunrise to sunset) is ~ 12.5 h and the average ambient daytime temperature nears ~35°C (Ali & Ripley 1999). In the remaining period, buntings seem to spend ~3 months each at breeding grounds and in to-and-fro migratory travels, totalling a distance of about 6000-7000 km (Ali & Ripley 1999; Ćiković *et al.* 2021).

Migratory phenotype

Each sub-annual LHS leading to the beginning and end of the migratory journey is exhibited in a distinct phenotype at multiple levels, including behavioral, physiological, neural and molecular. For example, the birds maintaining normal food intake and body mass during much of the year, begin showing an increased feeding (hyperphagia), accumulation of fat in the adipose and liver tissues to fuel the intense flight activity, and muscular hypertrophy to enhance flight endurance with transition from non-migratory to the migratory LHS. Along with, in most birds that undertake the migratory travel at night, the most distinct change in behavior is the development of nocturnality in the otherwise day-active species with transition from non-migratory to the migratory LHS. This requires a profound shift in behavior with the onset of the migration period (Berthold 1996; Bartell & Gwinner 2005; Rani *et al.*, 2006). In a caged situation, this is reflected by “wing whirring”, and called the migratory restlessness or *Zugunruhe* (Wagner 1930). *Zugunruhe* reflects the intensity as well as temporal pattern of actual migration (Czeschlik 1977; Berthold & Querner 1988).

Our research has shown that black-headed and red-headed buntings held captive under the natural daylength and temperature at their wintering latitudes in India (27° or 29°N) show migrant phenotype, identified most visually in the body fattening (accumulation of subcutaneous fat stores), body mass gain, and *Zugunruhe* akin to spring and autumn time nocturnal migratory flight (Gupta & Kumar 2013; Sharma *et al.*, 2022). Jain & Kumar (1995) monitored the black-headed buntings held captives in semi-natural variations of daylength and temperature in Meerut, India (29°N) for food consumption and body mass, and measured the size of gonads and plasma levels of luteinizing hormone, thyroxin and testosterone over a period for ~10 months beginning in January (thus study period covered both spring and autumn migration periods). There were seasonal cycles in all parameters that were examined, with a gain-loss cycle in body mass almost parallel with the testicular growth-regression cycle; however, the seasonal cycle in food consumption peaked much before the peak gain in body mass (Jain & Kumar 1995).

At the physiological level, the development of migratory phenotype is accompanied by significantly higher blood triglyceride levels, but not glucose levels, and growth and involution of specific internal tissues (Trivedi *et al.*, 2014). In black-headed buntings exhibiting the migratory phenotype, for example, the heart is significantly enlarged and weighs heavier while the intestine is significantly lighter in weight (Trivedi *et al.*, 2014). Concurrent hormonal changes include daily levels and rhythm in plasma insulin and corticosterone secretions (Mishra *et al.*, 2017). There is also a significant lipid accumulation in the liver in red-headed buntings exhibiting the migratory phenotype (Sur *et al.*, 2019).

Migration timing

Role of the prevailing environment

Among multiple environmental factors that restrict sub-annual LHSs to the best suited time of the year as well as shape diurnal changes in the behavior and physiology as per non-migrant and migrant periods, the most influential ones include variations in the daily light period (= photoperiod), ambient temperature and food availability (Kumar *et al.*, 2022). These three environmental cues may act in synchrony, and seasonal migration is possibly the net result of their mutually inclusive effects at multiple levels. Changes in the photoperiod and temperature concurrently affect the internal timing system, circadian and circannual clocks, and synchronize many biological processes to maximize reproductive success and eventually the species survival (Kumar *et al.*, 2010). Temperature influences the food availability more directly by its effects on humidity levels; thus, in turn, it affects the photoperiodic induction of seasonal LHSs (Kumar *et al.*, 2001; Visser *et al.*, 2009).

<u>Photoperiod:</u> Migrants are exposed to two types of photoperiod variations: daily changes in the time of sunrise and sunset at their inhabiting latitude, and latitude-dependent amplitude in variations because of wide differences in inhabiting latitudes across seasons. They stay for about one-third of the year at breeding grounds, *i.e.*, higher (temperate) latitudes, and overwinter for about half of the year at lower (subtropics/ tropics) latitudes; the remaining period in the year is spent in to-and-fro annual travels through consistently varying latitudes. In synchrony with prevailing photoperiod variations, the passerine migrants undergo sequential transitions from non-migratory to migratory to the non-migratory LHS, with intervening breeding and moult LHSs.

All migration-related phenologies are faithfully reproduced in captive buntings by manipulating the photoperiod length (Kumar *et al.*, 2022; Sharma *et al.*, 2022; Tripathi *et al.*, 2025). For instance, buntings held captives at the wintering grounds under a non-stimulatory short photoperiod which maintains the physiological state akin to that in late wintering period in the wild when exposed to a stimulatory long photoperiod (mimics increasing spring photoperiods; *e.g.* 10 h ⇢ 13 h light per day), exhibit the spring migration phenotype. Similarly, buntings maintained under a stimulatory long photoperiod in the physiological state akin to that in post breeding period in the wild, when exposed to a decreasing photoperiod (mimics autumn photoperiods; *e.g.*, 14 h ⇢ to11 h light per day) exhibit the autumn migratory phenotype (Trivedi *et al.*, 2014; Sharma *et al.*, 2018). The response to a stimulatory photoperiod can be very rapid; the transcription pathways involved in key biological processes underlying the hyperphagia, body mass gain, metabolism, cellular defence, which are identifiable features of the migration phenotype, are activated on the very first day of long photoperiod exposure in migratory buntings (Sharma *et al.*, 2021).

<u>Ambient temperature:</u> Variation in ambient temperature is concomitant with the photoperiod change; for example, nights are cooler than the day, and autumn/ winter gets progressively cooler than spring/ summer. Increasing evidence suggests the role of temperature in the development of migration phenologies in latitudinal passerine migrants, albeit with species and sex differences (Helm *et al.*, 2017; Sur *et al.*, 2019;

Trivedi *et al.*, 2019). For example, under a stimulatory 13-h photoperiod, black-headed buntings enhance muscle growth and advance the *Zugunruhe* appearance at 35°C, compared to 22°C temperature (Sur *et al.*, 2020). Along with, transcriptional responses suggest temperature effects on the multiple molecular drivers in both regulatory (hypothalamus) and effector (skin, liver, muscle) tissues, culminating in the migratory phenotype. Perhaps, the hypothalamus senses and integrates the ambient temperature information received/perceived by the peripheral (*e.g.*, skin tissues) temperature receptors (Sur *et al.*, 2020).

Food availability: In anticipation of the migratory departure, migrants undergo a period of hyperphagia in order to get an adequate fat fuel load for the upcoming migration flights (Odum, 1960; Blem, 1980, 1990; Newton, 2007; Trivedi *et al.*, 2014). This is species specific, and can account for as much as 100 % of lean body mass in small passerine migrants, for example, a much larger fat store is accumulated accounting for a much higher weight gain in the black-headed bunting than it is in the red-headed bunting even under identical photoperiodic manipulations (cf. Misra *et al.*, 2004; Rani *et al.*, 2005). In a more direct study examining functional linkage between food availability and migratory behavior, black-headed buntings were subjected to food availability such that they did not have food for 2h at the beginning and end of the light period, or had access to food during the entire light or dark period. When the timings of light exposure and food availability overlapped, the light masked the food effect, but food at night alone reduced both duration and amount of *Zugunruhe* (Singh *et al.*, 2012).

Role of internal clocks

The migratory departure at appropriate time (seasons) of the year is achieved by a close integration of internally recurring mutually coupled circadian (circa = about; dies = day) and circannual (circa = about; annum = year) rhythms with prevailing external (environmental) cues, *e.g.*, photoperiod (Kumar *et al.*, 2010; Stevenson & Kumar 2017). Circannual rhythms govern the timing of migration phenologies in interaction with the prevailing photoperiod (Gwinner 1986; Kumar *et al.*, 2010; Kumar & Mishra 2018). It appears that (i) the mechanisms underlying circannual rhythm generation and evolution of photoperiodism (*i.e.*, photoperiodic regulation of a biological event) are mutually inclusive, and (ii) the circannual migration program accommodates consistent variations in the photoperiod across season as well as along the migratory route (Misra *et al.*, 2004; Stevenson & Kumar 2017).

At the same time, circadian rhythm seems to be involved in daily changes in behavior and physiology as required during the migration. This is most obvious in a nocturnal migrant, which otherwise is a diurnal species. Underlying circadian rhythms regulating diurnal patterns in behavior and physiology seems to redefine itself with the onset of the migratory season (Bartell & Gwinner 2005; Rani *et al.*, 2006). This allows a diurnal species to fly at night, when it is cooler and the sky is relatively predator free. This suggests inherent flexibility in the internal clock system, which is evidenced by alterations in the waveform of circadian oscillations of *period 2, cryptochrome 1, brain muscle arnt like 1 (BMAL1), and circadian locomotor output cycles kaput (CLOCK)* genes that comprise the core of the molecular clockwork (Singh *et al.*, 2015). Indeed, 24-h clock gene oscillations show alterations in the acrophase and amplitude in both regulatory hypothalamus and effector liver tissues between photoperiod-induced non-migratory and migratory LHSs in migratory buntings (Singh *et al.*, 2015; Mishra *et al.*, 2017).

Energy management

Storage of fat fuel

An exceptionally high demand for energy during migration is met by the accumulation of fat fuel stores prior to migratory departure, albeit with species and population differences (Blem 1990). Some species fatten to the extent of gaining weight up to 100 % of the lean body mass, but others put on only a small weight with a little amount of fat. A varying degree of fat fuel storage appears linked to the foraging strategy, essentially differing between species those can replenish and those cannot replenish depleting energy stores (Biebach 1990; Bairlein & Simons 1995). A species with very low fuel stores will need feeding at stopovers every day en route to the migratory destination. Importantly, these fat stores get fully depleted, and birds return to their normal (lean) body mass once the migration is over. Interestingly, the lipid accumulation varies between spring and autumn; autumn migrants carrying a smaller fat fuel load. Spring migrants have a larger store of fat fuel, which they need to travel at a higher speed, with longer night-flight and shorter stopover durations (Bairlein & Schaub 2009; Newton 2007; Nilsson *et al.*, 2013; Yavuz *et al.*, 2015).

The fat fuel storage is mainly in the adipose and flight muscle tissues (Battley & Piersma 1997). There is a copious amount of fat deposits visibly seen lying subcutaneously. The pectoralis major and minor flight muscles also show increased lipid storage, and as a result, they are hypertrophied. There is also a change in the structure of muscle fibers at both the anatomical and molecular levels (Sharma & Kumar 2019; Sur *et al.*, 2019). More specifically, significant changes in the expression of myogenic differentiation 1 protein responsible for muscle differentiation (Legerlotz & Smith 2008; Zanou & Gailly 2013) and parvalbumin protein that quickens the relaxation-contraction ability of muscle fibres (Celio & Heizmann 1982) have been reported in migratory buntings (Sharma & Kumar 2019; Sur *et al.*, 2019).

Energy supply and efficiency

When in migration flight, migrants adapt to voluntary anorexia; conversely, they feed vigorously during the stopover period en route to their migratory destination. Per unit of time, avian migrants are in low-income and high energy expenditure state, as compared to when they are in the non-migratory and stopover period of high-income and relatively low energy expenditure state. Thus, a high metabolic turnover is needed to support the migration flight, which requires a strategy for overall energy homeostasis. This is exemplified by reduced energy expenditure by the onset of hypothermia and minimized activity prior to migration. Consistent with this, the energy supply sources, for example, carbohydrates and lipids, undergo significant seasonal fluctuations.

The major energy source is lipids, which when metabolized yield energy required for the migration flight. Indeed, circulating triglyceride levels show LHS-linked differences in migratory sandpipers (*Calidris mauri*: Guglielmo *et al.*, 2002) and black-headed buntings (Trivedi *et al.*, 2014). Increasing serum triglyceride levels correlate with pre-migratory body fattening in migratory songbirds (Guglielmo *et al.*, 2002; Jenni-Eiermann & Jenni, 1994; Williams *et al.*, 1999). However much less dependence is on carbohydrates as the energy source for migration. There is almost no change in blood glucose levels and expression of genes associated with carbohydrate metabolism between non-migrant and migrant periods in several migratory songbirds (godwits, *Limosa l. taymyrensis*: Landys *et al.*, 2005; Canada geese, *Branta canadensis interior*: Mori & George, 1978; sandpiper, *Calidris mauri*: Guglielmo *et al.*, 2002; blackcap, *Sylvia* *atricapilla*: Jenni-Eiermann & Jenni, 1996; robin, *Erithacus rubecula*: Jenni-Eiermann & Jenni 1996; red knot, *Calidrus canutus islandica*: Jenni-Eiermann *et al.*, 2002; black-headed bunting: Trivedi *et al.*, 2014).

The fuel supply for migration flight is from fat stores *via* free fatty acid (Ramenofsky 1990; Sharma & Kumar 2019). Sharma & Kumar (2019) found significantly higher blood levels of free fatty acids in migratory LHS in buntings. There is an exceptionally high rate of fatty acids oxidation in the liver and protein-mediated transport to 'working' muscles in order to generate and maintain the overall flux of energy as required consistently during the migration flight. This involves multiple regulatory steps, several transporter proteins (*e.g.*, fatty acid binding protein and fatty acid transporter/ cluster of differentiation 36) and enzymes, namely carnitine palmitoyl transferase, enzymes of the tricarboxylic acid cycle: malate dehydrogenase, α-ketoglutarate dehydrogenase (Guglielmo 2010). Trivedi *et al.*, (2015) found concomitantly increased citrate and malate dehydrogenase enzyme levels, suggesting an increased cellular metabolism, possibly by the oxidative phosphorylation, during migratory LHS in buntings. Importantly, corresponding to the seasonal LHS, the required metabolic alternations are regulated at the transcriptional level (Trivedi *et al.*, 2015). Thus, the transcription levels of genes coding lipid metabolism-associated proteins and enzymes in both liver and flight muscles can be contingent upon the metabolic requirements of the seasonal LHS. Indeed, the expression pattern of metabolism-associated genes shows significant differences between non-migratory and migratory as well as between spring and autumn migratory LHSs (Sharma & Kumar 2019).

Behavioral adaptation

Activity behavior

Change in daily activity-rest pattern is the most conspicuous alteration in behavior of migrants. There is a profound shift from diurnal to nocturnal activity pattern in many passerine migrants which are otherwise diurnal (active during the day and inactive at night). These birds travel several thousands of kilometers at night albeit with species-specific daytime stopovers in order to forage intermittently and replenish the depleted energy reserve (Berthold 1996). A GPS-based field study on long-distance avian migrants (rough legged buzzard *Buteo lagopus*, white stork *Ciconia Ciconia*, greater white fronted goose *Anser albifrons*, Himalayan vulture *Gyps himalayensis*) found that the activity period was strongly dependent on daylight exposure duration, irrespective whether they were ground foragers (storks and geese) or flying foragers (buzzards and vultures), or whether they reproduced in temperate (storks and vultures) or the arctic (buzzards and geese) zone (Pokrovsky *et al.*, 2021). The ground foragers showed an almost consistent activity throughout the daytime, while flying foragers changed uniformly their season-specific daytime activity with sun (Pokrovsky *et al.*, 2021). Notably, the drastic change in temporal activity pattern without necessarily a change in the overall daily activity seems a part of overall adaptive mechanism in a species for its nocturnal migration. Sharma *et al.*, (2018) found significant differences in both intensity and duration of *Zugunruhe* between photo-periodically induced spring and autumn migration phenotypes in captive buntings.

Food choice and feeding behavior

In preparation for the forthcoming migration, migrants eat more than what is required for keeping the body mass stable, switch to a more beneficial diet, and increase the assimilation efficiency (a more efficient assimilation of ingested food with reduced loss in excreta and feces). Many migrant birds show seasonal shifts in their food choice (Bairlein & Gwinner 1994; Bairlein & Simons 1995; Bairlein 2002). For example, a species feeding extensively on plants appears to rely more on lipids and less on proteins compared to those feeding extensively on arthropods. Likewise, several passerine migrants switch from fruits, the major or exclusive diet, in the pre-migratory period to an insect diet during the spring migration period (Izhaki & Safriel 1985; Bairlein & Simons 1995). There seem to be changes in both quantitative and qualitative availability of required food resources at stopover sites so that migrating individuals can replenish their depleted energy reserves, as required (Bairlein & Simons 1995). Interestingly, Mediterranean autumn migratory passerines show a shift from insect to fruit diet, but they completely rely on an insect diet during the spring migration period when fruits are almost entirely unavailable in the region (Bairlein & Simons 1995).

Conclusion and perspective

Twice-a-year, long-distance migratory travels of avian migrants represent a remarkable evolutionary adaptation strategy involving a careful coordination of the timing of migration, environmental responsiveness of physiological systems, and energy management. As a consequence, with the transition from non-migratory to migratory LHS, the obligate latitudinal migrants exhibit significant differences in behavior and physiology along with concurrent adjustments in the olfaction, visual and hypothalamic neural circuits. To support migratory flights, migrants utilize fat as a major flight fuel supplied by the adipose tissues *via* free fatty acids. The mechanisms underlying the generation and overall flux of energy involve the oxidation of fatty acids in the liver and concurrent protein-mediated transport to the 'working' muscles. Thus, there are neural and metabolic plasticities to respond to the prevailing environment, leading to seasonal homeostasis at both regulatory and effector system levels. Interestingly, there are differences between the two annual migrations, which differ in the timing, context, and prevailing environment. For example, spring migration requires a faster pace with fewer stopovers for timely arrival to be able to reproduce and raise offspring within a relatively narrow temporal window of favorable season. This translates into long nocturnal flights, and with relatively less time to re-fuel, spring migrants need to acquire a copious amount of fat stores before the migration flight. More so, males need to arrive earlier at the breeding grounds, in order to define their territories and build nests, which serve as key determinants of a successful reproduction. There can thus also be a sex-dependent strategy, at least for the spring migration. Next, migrants are in a different state of physiological responsiveness in relation to the prevailing environment. For example, in relation to the stimulatory effects of photoperiods, birds are in sensitive and refractory states at the beginning of spring and autumn migrant periods, respectively. Furthermore, migrating birds face differences in the direction of photoperiod (and perhaps temperature) change between two seasonal migrations–they experience consistently decreasing and increasing photoperiods during autumn and spring journeys, respectively.

This brings us to a few important questions at present. First, how the habitat loss affects the avian migration? Undeniably, along the migratory route, there is continued destruction of habitat, such as forest, wetland and coastal areas, along with the climate change. Alterations in temperature, weather conditions and food availability can significantly influence avian migratory patterns by shifting the timing and routes of migration. In addition, increasing urbanization, leading to a large part of the world experiencing brighter nights due to artificial lighting at night (lighted nights), is altering the temporal separation of day-night, which has been a key selection pressure in defining the biological processes. This can affect nocturnal migrants in multiple ways, including disorientation, migratory pattern disruption, and increased mortality rates during stopovers in urbanized environments. Therefore, it is important to assess whether and if so, how much these emerging environmental issues have begun posing threats to avian migrants. This, in turn, enables us to learn and make efforts systematically towards the conservation of habitats and the necessary conditions for birds to continue their successful annual migrations.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY

No additional data was used in this research.

AUTHORS' CONTRIBUTION

VK and VT conceived the idea and wrote the initial draft; VT and SK reviewed the draft. VK produced the final version. All authors approved the final version.

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