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NUTRITIONAL MECHANISMS AND TEMPORAL CONTROL OF MIGRATORY ENERGY ACCUMULATION IN BIRDS

F. Bairlein
Institut für Vogelforschung "Vogelwarte Helgoland", An der Vogelwarte 21, 26386
Wilhelmshaven, Germany

E. Gwinner
Max-Planck-Institut für Verhaltensphysiologie, Von-der-Tann-Strasse 7, 82346
Andechs, Germany

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INTRODUCTION

Migration, i.e. the seasonal movement between areas of breeding and distant sites of nonbreeding, is a common strategy of birds all over the world. It encompasses a wide variety of very different patterns and tactics (reviewed in

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2, 20, 36, 168). Migrations range from irregular irruptive movements as in crossbills *Loxia* sp. to regular short-to-medium distance migrations as in the dark-eyed junco *Junco hyemalis* or the European robin *Erithacus rubecula* to remarkable long-distance migrations over thousands of kilometers as in many species of warblers, thrushes, and waders. The most spectacular long-distance wanderers are arctic terns *Sterna paradisaea* that breed in the high arctic and winter off the Antarctic pack ice, more than 10,000 km south of the breeding grounds. Other notable long-distance migrants are found among shorebirds. Sanderlings *Calidris alba* and knots *Calidris canutus,* for example, travel from their circumpolar high arctic breeding grounds to wintering areas at coastal sites south to Patagonia, Southern Africa, Australia, and New Zealand. Not only large birds, but even very small songbirds may cover vast distances on their migratory journeys. A familiar species is the barn swallow *Hirundo rustica,* which breeds in the northern hemisphere and penetrates into the southern parts of America, Africa, and Asia. Similarly, some of the arctic warblers are transequatorial migrants, such as the willow warbler *Phylloscopus trochilus* and the garden warbler *Sylvia borin* in the Palearctic or the blackpoll warbler *Dendroica striata* in the Nearctic.

Many long-distance migrants must also cope with formidable ecological barriers such as oceans, mountains, and deserts. Such birds have developed a wide variety of strategies to adapt to these adverse conditions. Whereas some species or populations travel in short hops, others cover similar distances in jumps—very long flights with only one stop or none at all. The latter pattern is frequently found among oceanic migrants such as the Alaskan bristle-thighed Curlew *Numenius tahitiensis,* which winters exclusively on the small islands in the middle Pacific. Most blackpoll warblers from North America reach their Caribbean and South American winter areas by flying out over the Atlantic, departing from the northeastern coast of North America and reaching land again in the Caribbean and northern South America. The ruby-throated hummingbird *Archilochus colubris,* which weighs only 3 g, crosses the central Gulf of Mexico on a nonstop flight. Similarly, many European birds fly over the Mediterranean Sea while migrating to and from Africa. Several of these birds must cross the Sahara desert, a 2000 km stretch of very inhospitable land that obstructs the migration routes (62, 159, 172). Although most small migratory birds are active flapping flyers, some of the larger migrants, such as many raptors, storks, and cranes, rely on soaring in thermals for migration.

The physiological requirements and ecological constraints vary for birds using these different migration tactics. The extent of the migratory flights, the mode of migration, and the mode of flying determine the energetic demands of migration (e.g. 115, 191, 199, 200). A series of short flights requires fewer reserves; hence, less mass must be gained, and flying is thus less costly. On the other hand, a series of suitable stopover sites must be available. In contrast, migrating in long jumps is more expensive owing to the costs of carrying large amounts of extra fat, and the unavailability of one particular stopover site may seriously jeopardize the continuation of migration. This tactic may nonetheless prove advantageous because finding only one suitable stopover site requires less time than finding many successive ones. Furthermore, overall predation risk may be lower in the jumpers than in the hoppers as a result of the latters' many different unknown staging sites. Soaring birds use thermal upstreams to gain height and to migrate by energy-conserving gliding flights, although fasting during long-distance soaring is physiologically reasonable and may require some energy accumulation before departure (213).

The most conspicuous and general physiological adaptation to the energetic demands of migration is storage of energy-rich tissue. It is particularly pronounced in those species that cross vast inhospitable areas such as deserts or oceans where birds cannot replenish depleted stores and must therefore rely on endogenous reserves. The mass of stored reserves may amount to more than 100% of lean body mass (11, 27, 45–47). Because these reserves are required during precisely defined times of the year and because carrying large fat reserves has obvious costs, the appropriate timing of deposition is of utmost importance. It is not surprising, therefore, that migrants are equipped with a highly sophisticated timing system comprising both endogenous and exogenous components.

This review summarizes the known nutritional adaptations and the temporal control of migrants that enable them to cope with the enormous migratory energy storage in long-distance migration. We focus primarily on passerines because they are the largest group of migrants in all continents (141) and because most experimental work has been conducted on birds from this group. The review does not discuss migratory orientation, which was recently reviewed by Berthold (37), locomotion and flight performance (reviewed in 57, 179, 190, 191, 199, 200), the biochemistry and morphology of storage and utilization (reviewed in 46, 195, 197), or endocrine aspects of migration (reviewed in 227). Gwinner has further reviewed the physiology and ecophysiology of bird migration (101).

ENERGY RESERVES

With the exception of a few species that can feed extensively en route, e.g. terns, swallows, and swifts, migrants depend on internally stored energy and must therefore accumulate large reserves before or between migratory flights. Respiratory quotients measured in flying birds have revealed that carbohydrate is used primarily during takeoff and the first minutes of a migratory flight

(180, 205); little if any carbohydrate is used later on. The very high glycogen reserves found by Marsh (162) in premigratory gray catbirds *Dumetella carolinensis* may serve as the prime initial fuel for takeoff.

Proteins generally are not considered an important source of energy for migrating birds (46, 47). Early studies by Odum and colleagues (186) suggested that during the phase of premigratory body mass gain, body components other than fat remain essentially constant. However, subsequent investigations revealed that some increase in protein content may accompany the body mass gain (43, 59, 64, 72, 73, 78, 79, 193, 194, 223). Recently, Lindström & Piersma (158) reexamined published data and found that fat-free tissue deposition prior to migration is widespread among shorebirds. In many species, particularly larger ones, a considerable proportion (20–50%) of the migratory mass increase results from the incorporation of nonfat components (158, 194). However, the specific role of nonfat tissue, almost entirely protein, has not been fully elucidated. Most information on nonfat tissue deposition examined by Lindström & Piersma (158) refers to spring migration, but the extra protein carried by these birds may not have been deposited for migratory needs. Rather, as shown by Davidson & Evans (64) in shorebirds and by Ankney (5) in geese, most protein reserves deposited in spring are apparently carried to the arctic breeding grounds to ensure survival after arrival and subsequent reproduction. The few data on fall migrants revealed little or no protein accumulation for migratory purposes, and in some species fat alone is responsible for the total increase in body mass. Nevertheless, recent evidence strongly indicates that proteins fulfill specific tasks during endurance flights in migrating birds and may even serve as energy stores, particularly when lipid reserves are nearly exhausted (1, 19, 48, 129, 130, 158).

The major, if not general, store of energy for migration is fat (27, 45–47). Fat is mainly laid down subcutaneously within the body cavity; very little is stored in muscle and liver (195). The amount of lipid reserves is related to a bird's migratory distance (27, 47); short-distance migrants usually accumulate less fat than long-distance migrants. The amount of fat limits the length of a single migratory flight or that of the overall migration distance in birds migrating in a series of successive bouts interrupted by stopovers without feeding (12, 43, 63, 191). Apparently the largest fat reserves are accumulated in birds faced with huge ecological barriers that offer no opportunity to replenish exhausted energy stores. Some of these birds rely entirely on internal reserves of fat stored up before departure. Consequently, the mass of stored lipid can be rather substantial. For example, long-distance migrating garden warblers, which breed in Europe and winter in tropical Africa, weigh ~ 16–18 g during the breeding and wintering seasons but increase their body mass to as much as 34 grams before leaving for their trans-Saharan journey, both in fall and spring (15). Ruby-throated hummingbirds *Archilochus colubris* leave the northern Gulf of Mexico coast in the fall with a body mass double their normal lean mass (3 g; 152). Bar-tailed godwits *Limosa lapponica* increase mass at spring staging in the Dutch Wadden Sea by an average of 90% above nonmigratory levels (194). Small passerines had maximum fat deposition rates that reached 10-13% of lean body mass per day, with a proportional decrease with increasing body mass (156). Moreover, the daily rate of fattening, the fat reserves at departure, and stopover duration and behavior are determined in accordance with several optimization criteria (3, 122, 157, 171; see also 192).

Fat is primarily stored in the form of triacylglycerols (45, 197). The composition of adipose triglycerides is very important because the melting point of the fatty acids may influence ease of mobilization and use of the fat reserves (45–47). The most abundant fatty acids in the depot fat of birds are C_{16} and C_{18} molecules, which can comprise more than 90% of the total, with a preponderance of the unsaturated fatty acids oleic acid $C_{18:1}$ and linoleic acid $C_{18:2}$ (reviewed in 45–47). The influence of diet, age, sex, season, and physiological state on the fatty acid composition of adipose lipids is controversial (46). Similarly, the energetic significance of the unsaturated fatty acids has also been questioned (47). Nevertheless, these fatty acids may influence the melting point of lipid reserves and hence the net energy for mobilization of the fat depots (47, 133, 189).

NUTRITIONAL MECHANISMS TO ACHIEVE MIGRATORY FUELING

Among the mechanisms suggested for migratory fat deposition (46), nutritional mechanisms are obviously the most significant. The principal source of energy is food. The extra energy (costs) needed to accumulate reserves for long-distance migration has rarely been investigated. In shorebirds, a 1 g change in body mass requires on average an ~ 46 kJ increase in daily food consumption (142). In garden warblers, migratory body mass gain is associated with a daily net food intake (food metabolized) of 39 kJ/g body mass change on average (8). The thermal environment also affects energetic requirements for premigratory body mass gain (e.g. 148, 233). In any case, these costs must be met by nutritional mechanisms. Among the mechanisms listed (46), gross food intake (hyperphagia) has been the most extensively studied and is considered the most important. However, one must also take increased nutrient utilization into account (8). Increasing evidence points to an adaptive shift in diet and nutrient selection for migratory fueling, whereas evidence for other mechanisms (changes in basal metabolic rate, locomotor activity, and thermoregulatory capacities; reviewed in 46) is weak.

Food Intake and Assimilation

Premigratory increase of hyperphagia has been widely viewed as the key mechanism by which migratory fattening is achieved. In the white-crowned sparrow *Zonotrichia leucophrys* (143–146), the white-throated sparrow (184, 185), the bobolink *Dolichonyx oryzivorus* (81), the ortolan bunting *Emberiza hortulana* (222), the dark-bellied brent goose *Branta b. bernicla* (53), and the whimbrel *Numenia phaeopus* (231, 233), migratory fattening was said to result from a marked increase in daily food intake. However, other studies suggested a change in utilization efficiency as an additional mechanism. In the whitethroat *Sylvia communis*, the European robin *Erithacus rubecula* (169), the yellow wagtail *Motacilla flava* (79), the dickcissel *Spiza americana* (230), and the spotted munia *Lonchura punctulata* (40), hyperphagia alone cannot account for the observed mass gain; hence an increase of assimilation efficiency was proposed.

The insectivorous garden warbler was the subject of a more recent long-term study under controlled laboratory feeding conditions. The study demonstrated that both autumn and spring migratory fattening in this species was not only associated with a marked increase in daily food intake but also with a significant increase in the efficiency of food utilization (Figure 1; 8). Most of the variation in assimilation efficiency resulted from changes in the efficiency of fat utilization, but minor changes also occurred in carbohydrate and protein utilization. This enhanced efficiency significantly increased metabolizable energy and nutrient intake during migratory fattening compared with nonmigratory periods. Because these results were obtained in captive birds under controlled laboratory conditions, they indicate that endogenous control mechanisms corresponding to seasonal changes in the birds' physiological states are involved in the regulation of food intake and food and nutrient utilization. However, these regulatory mechanisms, including both behavioral (e.g. 218) and physiological traits (e.g. 138, 139, 147, 166, 176, 177, 188, 189, 197, 210), remain to be identified.

Seasonal Shifts in Food Selection

Many migrant species exhibit extreme seasonal shifts in diet selection during premigratory periods, although their adaptive role in migratory fueling has rarely been investigated (27–29, 45, 127). Geese feed selectively on a variety of specific plant species during migration, depending on particular nutrient requirements (e.g. 51, 68, 69, 167, 196, 198). Shorebirds may alter their diet selection during migratory stopovers (e.g. 232) and even eat seeds, which can comprise as much as 37% of the diet (21), or fruits (83). Chaffinches *Fringilla coelebs* change from an insect diet to a seed diet during fall premigratory fueling (67). Perhaps the most striking seasonal changes in diet composition

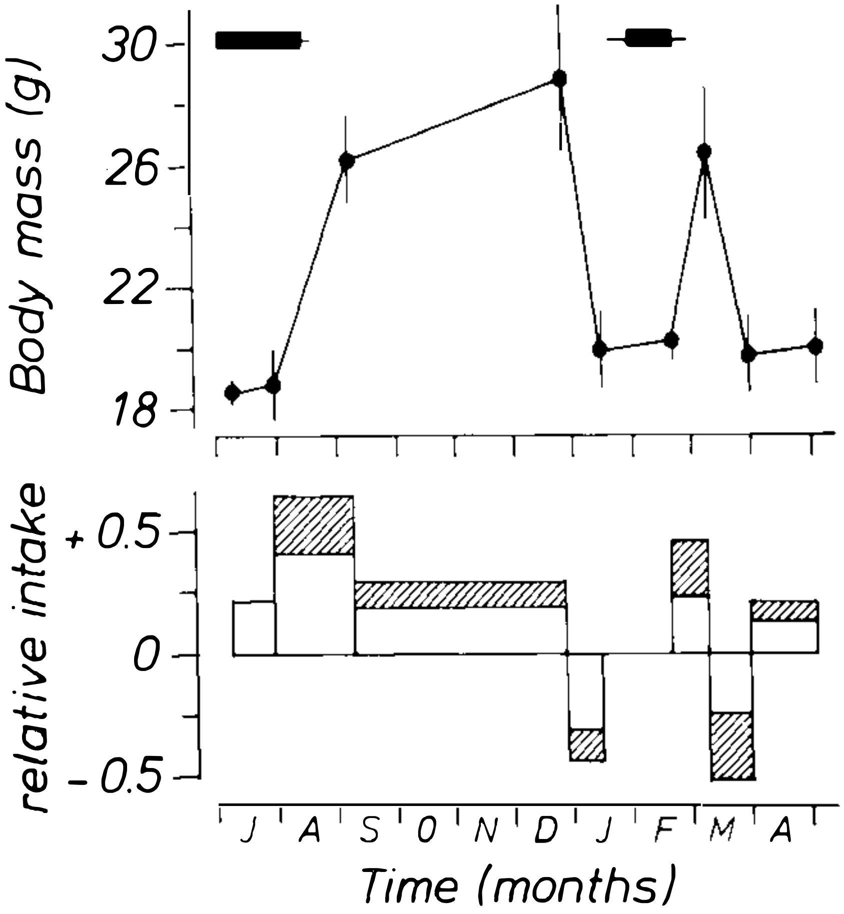

Figure 1 **Upper diagram: seasonal changes in body mass (curve) and occurrence of molt (bars) in a group of 10 captive garden warblers held in light:dark (LD) 12:12 at 20° C. Means with standard deviations are given. Lower diagram: net food intake of the same birds expressed relative to the low body mass phase in January and February. Open bars show changes in gross food intake (dry matter); dashed bars indicate the additional changes in net food intake resulting from changing assimilation efficiencies. For clarity, error bars of food intake are omitted. Drawn in accordance with data from Ref. 8.**

occur among passerine birds, which switch from a diet consisting almost entirely of insects in spring and summer to a diet comprising mostly—and sometimes exclusively—fruits during premigration or on the wintering grounds (e.g. 7, 52, 66, 77, 78, 80, 84, 85, 118, 119, 123, 134–136, 153, 173, 182, 207, 219).

SEASONAL FRUGIVORY Seasonal frugivory in migrants may sometimes simply reflect seasonal changes in the relative availability of insects and fruits. However, considerable evidence indicates that seasonal frugivory and seasonal dietary shifts in general are primarily the result of active changes in food preferences (13, 16, 46, 211, 212). Both the degree of frugivory during migration and the species-specific preferences for particular fruits often vary independently of local fruit abundance in the field (e.g. 7, 84, 126, 136, 151, 163, 164, 174, 220, 226). Even under controlled laboratory conditions with unlimited availability of various food items, selection (and the extent of frugivory) has undergone seasonal changes (Figure 2; 28, 29, 225; Bairlein, unpublished data). Moreover, in dual-choice feeding experiments with various berries and

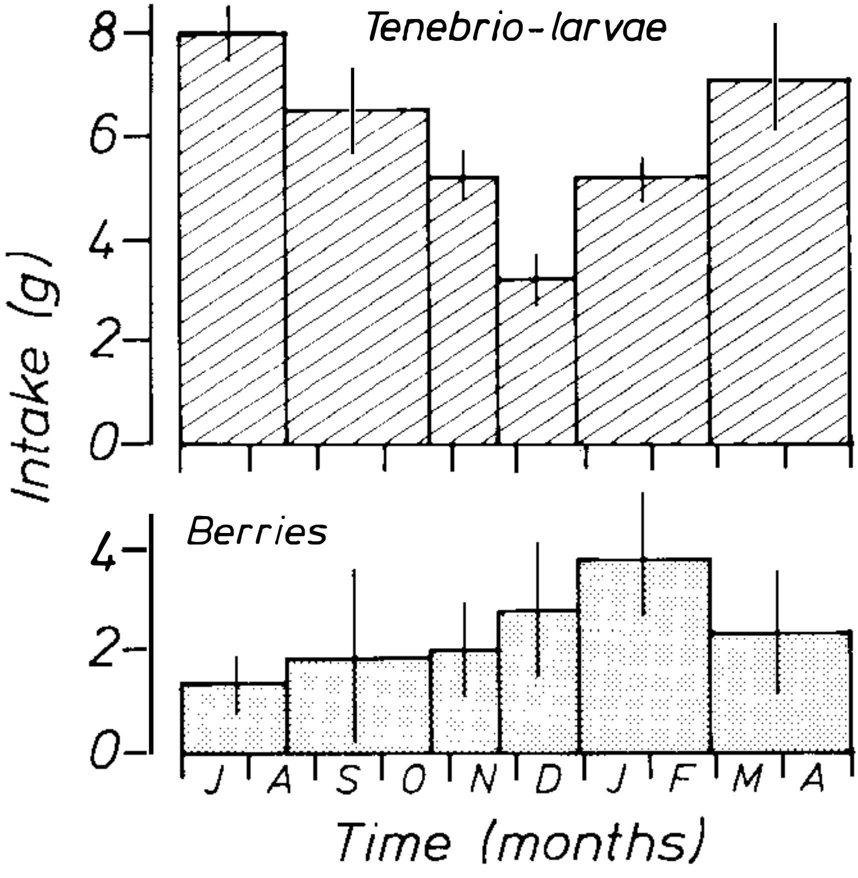

Figure 2 Seasonal changes in the intake of insects (Mealworm *Tenebrio* larvae) and berries in a group of captive garden warblers held in LD 10:14 at 20° C. Both foods were simultaneously available at all times (28).

fleshy fruits provided ad lib, garden warblers clearly preferred only some and avoided others (16, 212). Furthermore, they spontaneously reduced intake of insect food when berries were provided in addition (16). Thus, seasonal shifts in diet are associated with spontaneous changes in preference that correspond to changing nutritional requirements of the individual bird and to seasonal changes in the bird's physiological state rather than with responses to varying seasonal availability. Specific nutritional needs during migratory fattening may be better met by some foods than others. Consequently, the nutritional quality of food items may significantly influence foraging decisions in migrants (8, 55, 147, 198, 216, 217, 229).

It has often been proposed that the extent of frugivory in omnivorous species is limited by the paucity of nutrients, particularly proteins, in many fruits, which may prevent the birds from relying on fruits for long periods of time, especially for migratory fueling (28, 29, 118, 131, 139, 170, 174, 214, 224). However, recent studies revealed that garden warblers fed berries alone did not experience any significant long-term loss of body mass (14, 15, 212); in fact, they accumulated migratory fat, albeit at a slightly slower rate on average than conspecifics fed a nutritious insect diet. When warblers were fed a mixed diet of both insects and fruits, the daily rate of body mass increase was even higher than that of those fed insects alone (Figure 3; 18). These laboratory results are consistent with field data showing that fall passage migrants had significantly increased body masses at sites where fruits were available compared with sites without fruits (6, 15, 77, 80, 207, 219).

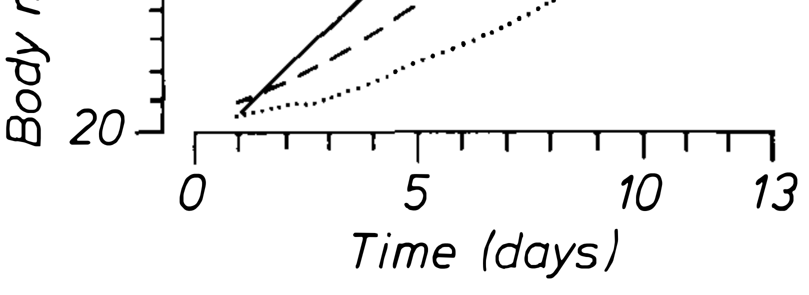

Figure 3 Changes in body mass of garden warblers fed either a pure insect diet (n = 7), a pure fruit diet (figs; n = 7), or a mixed diet of insects and fruits (n = 8). For clarity, error bars are omitted (211).

Feeding experiments with garden warblers revealed dramatic disparities in the effectiveness of different fruits (16). Even the berries of closely related plant species, e.g. black vs red elder *Sambucus nigra, S. racemosa,* had rather different effects, despite the fact that both berries are relatively similar in nutritional value (28). Whereas birds fed only black elderberries successfully deposited migratory fat, those fed red elderberries experienced a drastic loss of body mass (16, 212). These observations indicate that the as yet unidentified particular quality of the fruits must be considered.

SECONDARY PLANT METABOLITES Secondary plant metabolites can control feeding of herbivores or frugivores by acting as plant defensive compounds and feeding deterrents. These affect both the availability of nutrients, particularly proteins, and the activity of digestive enzymes or symbiotic microorganisms and can even damage the digestive tract (e.g. 50, 54–56, 124–126, 128, 137, 139, 140, 154, 155, 161, 175, 201–204, 208). Counteradaptations of wild birds to plant allelochemicals have been poorly studied, but such adaptations take place in invertebrates (e.g. 22, 181) and are becoming evident in mammals as well (187). Recent evidence suggests that wild birds may also be able to cope with defensive plant compounds (54, 132, 149, 150, 183). Moreover, observations in garden warblers (14, 16, 18, 211) and white-crowned sparrows (71) revealed that some plant secondary metabolites may even stimulate food intake and metabolism. Evidence suggests that the increased appetite characteristic of birds feeding on fruits results from allelochemicals consumed with the fruits. Garden warblers fed an artificial synthetic fruit diet simulating the energy and nutrient content of black elderberries but devoid of secondary plant metabolites exhibited a considerable decrease in body mass compared with those fed actual berries. Conversely, conspecifics fed a diet supplemented with small amounts of a homogenate of black elderberries containing secondary metabolites that did not alter the dietary energy or nutrient content exhibited an almost 50% increase in daily food intake and a continuous though slight daily increase in body mass (18, 211). The mechanisms by which secondary plant metabolites affect food intake and the accumulation of depot lipids remain unknown, and the factors governing diet selection and fruit intake also need to be clarified.

NUTRIENT COMPOSITION In addition to secondary plant chemicals, the specific quality of nutrients may also affect diet selection, food intake, and metabolism. Garden warblers simultaneously fed two diets identical in gross lipid content but different in fatty acid composition of lipids exhibited clear preferences for foods rich in C_{18} unsaturated fatty acids (16). Feeding birds with a pure C_{16} fatty acid food impaired refattening following food deprivation (Figure 4; 18). The preference for C_{18} fatty acid foods is particularly interesting,

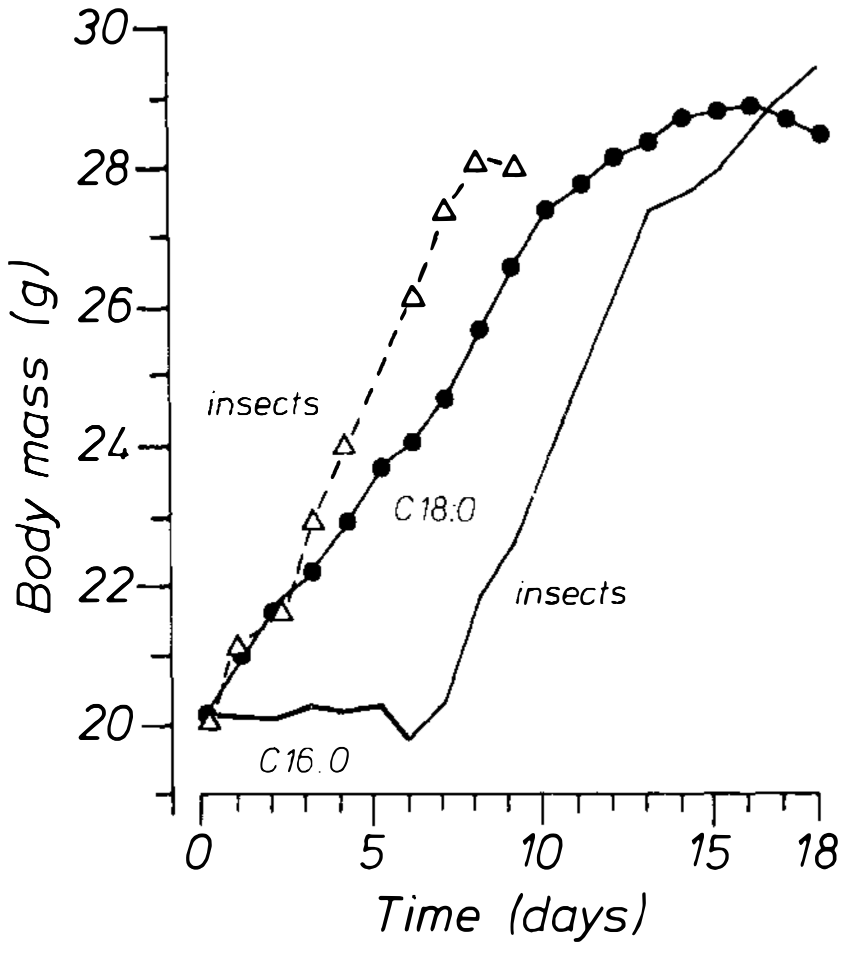

Figure 4 Changes in body mass of garden warblers fed either a pure insect diet or a diet containing either pure palmitic ($C_{16:0}$) or stearic ($C_{18:0}$) fatty acid lipids (n = 6, for each group). For clarity, error bars are omitted (Bairlein, unpublished data).

because C_{18} fatty acids are normally predominant in the depot lipids of free-living garden warblers (16) and other species (45, 46). For species that must achieve high rates of lipid accumulation, it may be very adaptive to preferentially incorporate these particular fatty acids directly from their food, thus reducing the energy costs for tissue deposition. Because plant lipids are generally rich in unsaturated C_{18} fatty acids (e.g. 4, 221), seasonal shifts of diet selection and facultative seasonal frugivory may represent a specific strategy to promote the accumulation of premigratory fat of a particular quality (45, 197, 206). In nonfrugivorous species, selection for phytophagous invertebrate prey rich in plant-originated fatty acids may also promote fat deposition. Selective absorption of ingested fatty acids by the intestine may also occur (197). In regard to the specific role of dietary lipids, many fruits in the Mediterranean region, where many of the trans-Sahara migrating Palearctic passerines fatten during fall migration, appear to be generally higher in lipids than fruits in the temperate zone (65, 119, 120, 215). The seasonal occurrence of several migrant frugivores coincides with a predominance of these lipid-rich fruits (118).

NUTRIENT SELECTION In addition to distinguishing between foods differing in fatty acid composition, migratory birds can sense other specific nutritional qualities and hence make appropriate choices to meet their nutritional requirements. Northern mockingbirds *Mimus polyglottus*, gray catbirds *Dumetella carolinensis* (49), garden warblers (13), and European robins (116, 117) preferred fruits high in fat content to those low in fat. High dietary fat levels may reduce the costs of premigratory lipid accumulation because they may enable migrants to incorporate fatty acids directly from their food (27). However, white-throated sparrows *Zonotrichia albicollis* could not make such distinctions (49), which suggests that various species differ in this capacity. Furthermore, feeding of geese at staging during migration depends on particular nutrient demands, which influence diet selection (e.g. 51, 55, 60, 69, 196, 209).

NUTRITIONAL CONSTRAINTS OF FRUGIVORY The extent of frugivory in omnivorous birds may be limited by the fact that many fruits contain only small amounts of dietary proteins. However, birds can respond to a low dietary nutrient content with a compensatory increase in food intake and nutrient assimilation efficiency. This response enables them to recover quickly from an initial transitory loss in body mass (10) by detecting specific nutrient deficiencies and effectively regulating the intake of specific diets and nutrients. Thus they can avoid malnutrition and adapt rapidly to changing nutritional demands and food resources during migration (147, 165, 176). Moreover, garden warblers that had adapted to very low dietary protein levels such as those found in many fleshy fruits consumed in the wild had much lower daily protein requirements than previously suggested (10). The birds' adaptability is obviously much higher than previously assumed (28, 29, 127; see also 223).

Because many fruits are rich in carbohydrates (65, 119, 131, 170, 214, 215), insectivorous or carnivorous species may shift to such foods to facilitate migratory fat deposition (21, 67, 83). Even selective feeding on aphids observed in warblers during migratory stopovers may be related to the high sugar content of these insects (41, 82).

Reliance on fruits during migration appears to be a significant adaptation.

Fruits are often locally superabundant, which minimizes the time spent searching for food. Moreover, they are easy prey (215): Because of their generally low fiber content, fruits seem to require relatively little mechanical breakdown to reach the nutritious cell content (170). Fruits also seem to be rich enough in nutrients to meet the specific physiological needs of feeding migrants, and the toxicity of fleshy fruits can be counteradapted by birds. In this context, one must remember that the available information on toxicity is almost completely derived from humans and thus does not necessarily reflect the degree of toxicity in birds (70, 183).

TEMPORAL CONTROL OF MIGRATION AND MIGRATORY FATTENING

Numerous studies on a variety of species have indicated that the major environmental factor controlling the migration and migratory fattening processes—as well as many other seasonal phenomena (molt, reproduction, etc)—is photoperiod. In general, long photoperiods induce or advance spring fattening, whereas fall fattening frequently requires short photoperiods. However, fall migratory disposition appears to develop independently of immediate photoperiodic stimulation in certain species in which fall migratory disposition may be a delayed consequence of stimulation by the long photoperiods of the previous spring (reviewed in 35, 39, 74–76, 92, 102, 103, 178). This observation implies that at least some of the events involved in the temporal control of migratory behavior can proceed in the absence of acute environmental changes, i.e. according to an endogenously preprogrammed pattern.

Spontaneous endogenous processes have indeed been described for a variety of migratory species, not only with regard to the onset of fall migration but also for the preparation and onset of spring migration. Research in this area has led to the discovery of endogenous rhythms that may run for many years in the absence of seasonal photoperiodic changes (reviewed in 34, 35, 89, 91, 92, 94, 95, 103). These endogenous oscillations can be modified by two groups of environmental factors: (*a*) photoperiod, which as a true Zeitgeber affects the oscillation itself, synchronizing it with the natural year and adjusting it to prevailing conditions, and (*b*) a host of other factors that modify the biological functions controlled by the circannual oscillator without affecting the oscillator per se. This concept has proven useful for understanding, predicting, and testing ideas about the temporal control of migration, including its energetic and nutritional adjustments (reviewed in 34, 89, 92, 94, 95, 99, 102, 103).

The Circannual Component

Circannual rhythms exist in ~ 50 species of organisms of many taxonomic groups, ranging from lower plants (160) to mammals (reviewed in 95). These rhythms have been shown to exist in several species of migratory birds, such as *Phylloscopus* and *Sylvia* warblers, flycatchers, and finches (see 8, 58, 95, 121). Studies of these migratory birds involve demonstrations of endogenous circannual cycles in migratory restlessness (e.g. 8, 25, 26, 37, 86, 93, 111), orientation (112, 113), and fattening (e.g. 8, 25, 26, 31, 37, 93, 111) as well as in associated changes in the amount and quality of ingested food (Figure 1; 14, 28) and in the efficiency of food assimilation (Figure 1; 8). Some of these rhythms persist for many cycles under constant conditions. As a rule, the period of these oscillations deviates from exactly one year, attesting to their true endogenous nature. Several comparative studies, e.g. on *Phylloscopus* and *Sylvia* warblers, flycatchers, and stonechats *Saxicola rubetra,* suggest that the endogenous circannual mechanisms controlling migratory parameters are particularly well developed in long-distance migrants, which must adhere to a tight seasonal time schedule and which, as a consequence of their migrations across latitudes, are exposed to peculiar photoperiodic patterns.

Endogenous mechanisms presumably stabilize the control system against the noise inherent in exogenous seasonal synchronizing cues. At the same time, they ensure appropriate timing of activities during seasons in which birds live in seasonally constant or unpredictable environments. For example, as for the preceding winter molt, these circannual mechanisms strictly control the development of spring migration and the associated fat depositions in willow and garden warblers wintering close to the equator (e.g. 39, 94, 95, 103).

Synchronization by Photoperiod

In all species studied to date, by far the most important—and possibly the only—Zeitgeber is the annual cycle in photoperiod. This has been demonstrated most convincingly in experiments that exposed birds to photoperiodic cycles with periods deviating from 12 months (e.g. 6-month cycles). As a rule, the period of the birds' biological rhythms followed the altered period of the photoperiodic cycle (91, 92). In addition to molt and various reproductive parameters, the annual rhythms of migratory restlessness and fattening have thus been shown to synchronize to photoperiodic cycles (reviewed in 95). However, several deficiencies have been observed in the circannual cycles in fat deposition (see below).

Photoperiod synchronizes circannual rhythms by affecting angular velocity in a phase-dependent manner. The way in which particular fractions of the birds' annual cycles are accelerated or decelerated by photoperiod is often of functional significance. Thus, short photoperiods usually accelerate the development of autumnal migratory behavior and fat deposition. This effect ensures that young birds born late in the year, which on average experience shorter photoperiods than birds born earlier, will start migration in time, i.e. before autumnal conditions become too severe for survival. Conversely, long photoperiods accelerate the onset of migration in spring, at least in equatorial and transequatorial migrants such as garden warblers and collared flycatchers

Ficedula albicollis. Again, this effect is of functional importance. It allows an earlier onset of spring migration in those individuals of a population that happened to migrate furthest south during the preceding fall migration and therefore must cover a longer distance on their journey back to the breeding grounds. Individuals wintering further south are exposed to longer photoperiods than those wintering in the more northern part of the range; hence, the accelerating effect of long photoperiods appears to keep the circannual program in step with the seasons (32, 37, 95, 103).

Although long photoperiods accelerate the time course of events leading to spring migration, the system is not fully advanced. Even under the simulation of a very long photoperiod characterizing winter quarters at 20° south, spring migratory restlessness and fattening of garden warblers are advanced by no more than six weeks compared with conspecifics held in an equatorial photoperiod (97). This weak response to long photoperiod prevents reproduction in the southern hemisphere summer. It results from the specific design of the mechanism controlling these birds' refractory state (98, 107).

Although garden warblers and collared flycatchers exhibit adaptive responses to a wide range of photoperiods during the winter season, other long-distance migrants do not. This observation is exemplified by studies on the pied flycatcher *Ficedula hypoleuca*, a species closely related to the collared flycatcher. The wintering range of the collared flycatcher lies relatively far south, extending from ~ 10° north to 20° south, whereas that of the pied flycatcher is restricted to the tropical zone just north of the equator. If exposed in winter to photoperiods characteristic of equatorial or southern hemisphere areas, its circannual oscillation is arrested; i.e. spring migratory disposition never develops and gonads remain inactive. These birds must experience a photoperiod shorter than that characteristic of a wintering range slightly north of the equator before rhythmicity can resume. The failure of pied flycatchers to continue cyclicity under long photoperiods has been traced to their failure to terminate refractoriness under long photoperiods. Only the collared flycatcher with its more southerly wintering range has evolved its photoperiodic response system in such a way that photorefractoriness can be terminated under these extremely long day lengths (99). Taken together, these studies show that endogenous circannual cycles and exogenous photoperiodic stimuli constitute a functional entity: The circannual programs respond to photoperiod in a manner that ensures optimal adjustment to season and latitude. Photoperiods outside the range of day lengths normally experienced by birds of a particular population may result in the arrest of rhythmicity (100, 102).

Species- and Population-Specific Programs

Comparative investigations of a variety of warblers of the genera *Sylvia* and *Phylloscopus* have indicated that the pattern of fall migratory restlessness developed by first-year birds reflects to a certain extent the patterns of actual migration: The further a species (or population) migrates, the higher the overall degree of migratory restlessness developed by individuals of that taxon under cage conditions (24, 34, 87, 94). Even details of the time course of migration may surface in the pattern of migratory restlessness measured under cage conditions (33).

Evidence derived primarily from comparative studies of closely related species with different migratory habits suggests that circannual programs may also predetermine onset, amplitude, and various other aspects of migratory fattening. For example, when central European pied and collared flycatchers were kept in the same controlled cage conditions, collared flycatchers attained slightly higher maximal body weights during the fall migratory season than pied flycatchers (111). This difference may partly reflect the fact that European collared flycatchers migrate over a slightly longer distance (to equatorial and southern Africa) than pied flycatchers (to areas north of the equator). Moreover, collared flycatchers cross the Sahara desert, whereas pied flycatchers tend to migrate along the western edge of the Sahara, where they presumably have more frequent opportunities to refuel.

Under experimental conditions, these two species not only differed with regard to maximal body weight, but also with regard to the time course of fattening. Whereas the pied flycatchers (like many other migrants) began to deposit fat relatively early in the season, at about the time of onset of migratory restlessness, the collared flycatchers began depositing fat much later, long after the onset of migratory restlessness. However, subsequent fat deposition in collared flycatchers occurred at a very rapid rate (Figure 5).

This exceptional pattern of fattening presumably corresponds to the collared flycatchers' peculiar migratory performance. Ringing data suggest that birds from the populations studied leave their breeding grounds at a very early age, possibly as early as July, to slowly migrate to southern Italy, where they apparently remain until September or early October before beginning their trans-Mediterranean and trans-Sahara flight. The dramatic increase in body fat probably occurs just before takeoff and is favored by ideal feeding conditions in the northern Mediterranean area (111).

The interpretation given above for the different fattening patterns of the two flycatcher species is uncertain, mainly because field data on fat loads of migratory flycatchers are insufficient for direct comparisons. Lack of field data is a frequent obstacle in the evaluation of experimental results, and predictions about endogenous patterns often rest on assumptions. One of the more likely predictions, which is supported by some field data (compare with 2), is that long-distance migrants should generally deposit more fat and should remain fat for a longer time than short-distance migrants. Comparative studies on

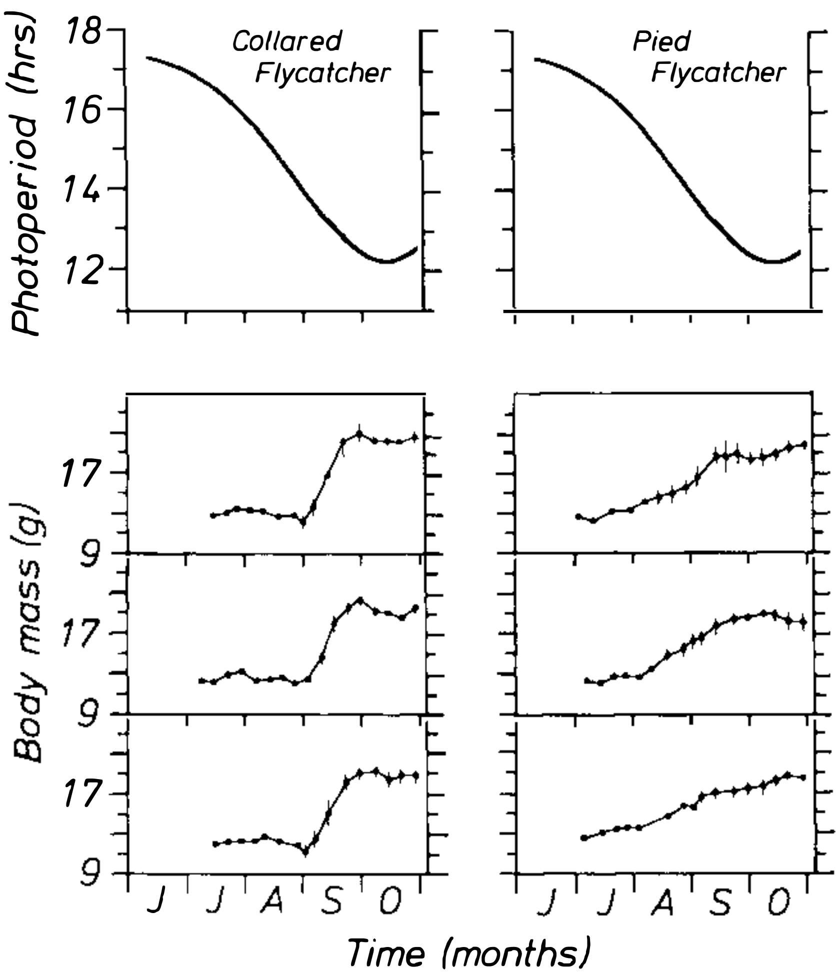

Figure 5 Seasonal changes in body mass in three groups of captive collared flycatchers (*left*) and pied flycatchers (*right*) held in autumn under the photoperiodic changes shown in the upper two graphs (99).

Phylloscopus and *Sylvia* warblers (26, 37, 88, 104) have confirmed this prediction. Even birds from populations of the same species migrating over varying distances may exhibit the predicted differences in maximal amount (black-capped *Sylvia atricapilla*) or duration (red-backed shrike *Lanius collurio;* 105) of autumnal fat deposition. In several of these studies, the compared birds were held in the same constant photoperiods, which strongly suggests that the observed differences result from endogenous differences in circannual organization.

Another prediction based on field evidence is that fall fat deposition should begin earlier in experiments with long-distance migrants (which usually begin migration early) than in those with short-distance migrants (which usually begin migration late). Again, several experimental results obtained with either changing or constant environmental conditions verify this prediction (e.g. 37, 38, 90, 104).

Although the data presented thus far indicate that the characteristic fattening patterns of migratory birds during fall migration are to some extent endogenously preprogrammed, some discrepancies are inherent in this concept. Caution is therefore advisable in evaluating the role of the endogenous circannual component. During the fall migratory season the body mass of long-distance migrants often remains high for a much longer time in caged birds than in free-living conspecifics. In caged garden warblers, for example, body mass usually increases steadily throughout the fall migratory season and eventually drops rather sharply around the onset of molt in the middle of winter, long after fall migratory restlessness has declined (Figure 1). Conversely, in free-living garden warblers body mass is maximal after the first third of the migratory season (shortly before the Sahara crossing) and subsequently declines while the birds are still migrating (15). Inappropriate simulation of photoperiodic or other conditions cannot account for these dramatic differences. The extended phase of fattening may be related to the fact that caged birds expend much less energy than free-living birds during the fall migratory season. Alternatively, caged birds may not receive significant environmental stimuli, which terminate the state of migratory fat deposition in free-living conspecifics.

Discrepancies between fattening patterns of caged and free-living birds are particularly striking during the spring migratory season. Although many data suggest that free-living migrants deposit as much or even more fat in spring than in autumn (15), caged birds often deposit little or no fat during the spring migratory season (Figure 1; 8, 9, 33, 37, 111, 113). Results obtained from garden warblers suggest that this truncation or abolition of spring fattening in caged birds may result from the inhibitory effects associated with a prematurely activated hypothalamo-pituitary-gonadal axis: A comparison of caged warblers exposed in winter to different photoperiodic conditions revealed that groups of warblers in which gonads had begun to develop immediately after termination of winter molt did not exhibit spring fattening, whereas birds with delayed gonadal development did. Within these groups the duration of fattening was positively correlated with the interval between the termination of molt and the onset of gonadal growth (96). Inhibition of vernal fattening by factors associated with an activated hypothalamo-pituitary-gonadal axis may be one of the mechanisms that terminates the obese state in spring migrants that have reached their breeding areas (228). In caged birds this axis may develop more rapidly than in free-living birds because in the latter, factors associated with actual migration may inhibit its rapid development (23).

Body Reserves and Migratory Activity

Although the states of migratory activity and migratory fattening are usually closely associated temporally, many data indicate that the former does not depend on the latter in a simple and direct way. This evidence is derived from the following observations: (*a*) Spring migratory restlessness developed normally in garden warblers that did not fatten during the spring migratory season (33, 37, 111, 113). (*b*) In garden warblers that passed through repeated circannual cycles under constant photoperiodic conditions, migratory restlessness and fattening sometimes became completely dissociated, i.e. they were no longer in phase (37, 108). (*c*) Preventing birds from becoming fat at the beginning of the fall migratory season had no effect on the development of migratory restlessness (30, 31). (*d*) Starving birds to low fat levels at the height of the migratory season resulted in only a slight increase in migratory restlessness; this effect was most conspicuous toward the end of the migratory season (42, 106, 109). This mechanism presumably stimulates birds in which the internal migratory program has almost run down but that have not yet reached acceptable nutritional conditions to continue migration (11, 44).

Although these results indicate that migratory activity is to a remarkable degree independent of both fat load per se and its reduction, factors associated with increasing body mass exert dramatic effects: As first described for the spotted flycatcher (*Muscicapa striata;* 42) and subsequently for the garden warbler (106, 110), migratory restlessness is entirely abolished while birds rapidly accumulate body weight following a period of spontaneous or induced body mass loss (Figure 6). Suppression of migratory activity in birds that have the opportunity to refuel after losing fat reserves is an important mechanism in the control of migration. It explains field observations that migratory birds arriving at resting places with depleted fat reserves tend to stay and refatten if feeding conditions are favorable but tend to continue migration when conditions are unfavorable (8, 11, 17, 42). Which of the many factors associated with refattening plays the key role in stopping restlessness remains unclear. In principle, any process in the spectrum, ranging from behavioral food uptake to endocrine processes associated with feeding or digestion to a combination of these factors, may be involved. The simple experimental paradigm of food-depriving and refeeding birds, thereby stopping and restarting migratory

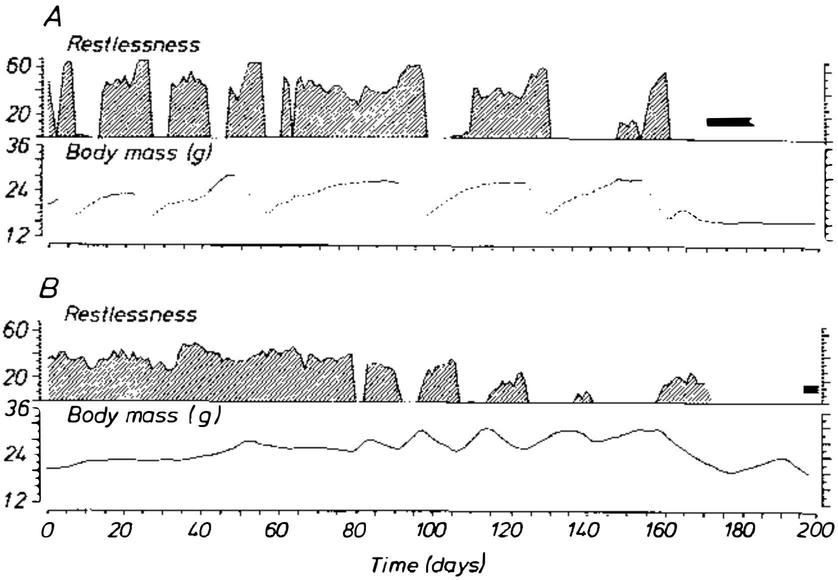

Figure 6 Variations of migratory restlessness (expressed as 10-minute intervals with nocturnal activity; *hatched areas*) and body mass (*curves*) as well as occurrence of molt (*bars*) of two garden warblers. Birds were held from September 1 (day 0) under photoperiodic conditions simulating those normally experienced by free-living conspecifics. Bird A was food-deprived during the times indicated by the dotted fractions of the body mass curve; it received 8 g/day of food during the time indicated by dashed fractions and food ad libitum during the time indicated by the unbroken fractions. Bird B exhibited spontaneous body mass changes while food was continuously available ad libitum (110).

restlessness, should prove useful in analyzing the physiological mechanisms that control and modify circannual time programs.

CONCLUSIONS

The results summarized in this review reveal that migratory birds are equipped with a variety of specific nutritional mechanisms that evolved to cope with the particular energetic demands of migration. These nutritional mechanisms are appropriately adjusted to other functions related to migration, i.e. migratory activity, as well as to other seasonal events, such as molt and reproduction. These adjustments are achieved by the action of both endogenous and exogenous timing factors, including photoperiod and circannual components.

However, the success of migration is not only determined by these central mechanisms but also by the availability of appropriate food resources, in terms of both quantity and quality, at staging sites along the migratory route. Adequate staging sites are therefore prerequisites for the survival of many migratory bird species. Conservation activities at both the national and international levels must ensure that crucial and vulnerable areas are identified and protected to support migratory birds in their travels across countries and continents (61, 114).

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