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REVIEW ARTICLE

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How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds

Abstract Many migratory birds accumulate large amounts of lipids as the prime energy source for their long-distance flights. This fat accumulation is mostly under endogenous control, reflecting genetically programmed temporal shifts of the body mass set point. It is accompanied by an increase in daily food intake and food utilisation efficiency and by a seasonal shift in food selection. In particular, seasonal frugivory appears to play a key role in many migrants. Fruits have a high content of fatty acids indispensable for building up the specific depot lipids. In addition, plant secondary compounds seem to play some kind of supportive role, but the mechanisms are not yet known. The effect of being fat on the metabolic situation in migrant birds appears to be similar to the metabolic syndrome in obese humans. The fat migratory bird provides a model through which to study nutritional factors as well as the biochemical and endocrine regulation of food intake, body mass and obesity.

Introduction

Migration is energetically costly. With the exception of a few species that are able to feed extensively en route, e.g. terns or swifts, most migrants depend on internally stored energy and must therefore accumulate large stores before embarking on long migratory flights. Within a couple of weeks, migrants can double their body mass. Species crossing inhospitable areas such as seas and deserts with no feeding opportunities accumulate large amounts of energy stores prior to their endurance flights. The garden warbler, *Sylvia borin*, for example, a long-distance European migratory songbird wintering in tropical Africa, weighs about 16–18 g during the breeding and wintering seasons, but increases its body mass to up to 37 g just before leaving to cross the Sahara, both in autumn and spring (Bairlein 1991a). The average bar-tailed godwit (*Limosa lapponica*) increases in mass during spring staging in the Dutch Wadden Sea to 90% above its non-migratory level (Piersma and Jukema 1990). Maximum fat deposition rates were found in small passerines with up to 10–15% change in lean body mass per day (Bairlein 1987a; Lindström 1991).

In contrast to previous ideas that body stores of migratory birds consist almost entirely of fat (Odum et al. 1964), recent data suggest that changes in body mass preceding migration also involve a change in lean body mass. Nevertheless, in small passerines, typically some 70–80% of body mass gain is due to lipids (Lindström and Piersma 1993; Klaassen and Biebach 1994; Klaassen et al. 1997; Bauchinger and Biebach 1998). In waders, migratory mass increase consists of some 35% nonfat, mainly protein, components (Lindström and Piersma 1993; Battley et al. 2000). The role of the protein stores is still a matter of debate (Bairlein and Totzke 1992; Jenni and Jenni-Eiermann 1998; Bauchinger and Biebach 1998), from an energetic point of view, however, they account for less than 5% of the energy expenditure (Blem 1990; Bauchinger and Biebach 1998). Carbohydrates are used to fuel takeoff and the first few minutes of the flights but not endurance flights (Nachtigall 1990). Thus, the prime energy for migration derives from lipids which are mainly stored subcutaneously; very little is stored in muscle and liver (Pond 1978; Bauchinger and Biebach 2001). Fat accumulation is thus one of the most spectacular physiological preparations for migration. The amount of fat stores is related to the distance the birds have to cover (Berthold 1996).

Seasonal migratory fattening is due to endogenously programmed circannual shifts of a body mass set point (e.g. Gwinner 1986; Bairlein and Gwinner 1994; Berthold 1996). Even in captivity under constant environmental conditions, migrants show spontaneous seasonal patterns of body mass change similar to their wild conspecifics (Fig. 1). There is no evidence that the body composition of the birds in captivity differs much from birds in the wild (Hume and Biebach 1996; Bauchinger

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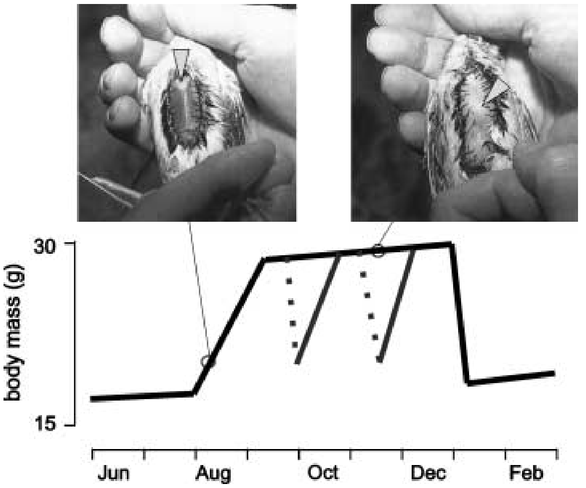

Fig. 1 *Top:* A relatively lean garden warbler (*left*) weighing about 18 g would not be able to undertake long flights, unlike the fat bird (*right*) weighing about 30 g and well prepared for its trans-Saharan journey to Afro-tropical wintering grounds. The *arrows* indicate subcutaneous fat (photograph by F. Bairlein). *Bottom:* Spontaneous seasonal fat accumulation in captive migratory garden warblers. If birds are food restricted during the phase of seasonally high body mass (*dotted line*), they immediately return to their seasonal set point of body mass when ad libitum feeding is resumed

and Biebach 2001; U. Totzke and F. Bairlein, unpublished). The onset and amplitude of migratory fattening observed in captivity are an accurate reflection of the natural variation in migratory distances and strategies of different species, and even birds from populations of the same species migrating over different distances show differences in maximal amount or duration of autumnal fat deposition. Moreover, as long as the internal migratory status is maintained, fat birds that have experimentally been mass-reduced by food restriction or deprivation always return to the high body mass level upon normalisation of the feeding conditions (Berthold 1976a; Fig. 1).

However, external triggers controlling the migratory fat accumulation in these basically internally driven long-distance migrants must also be considered. In garden warblers, short-term food shortage has been found to stimulate autumnal fattening, owing to a catabolic impulse being imposed by decreased food availability (Totzke et al. 2000). Similar results have been obtained in migratory hummingbirds (Hiebert 1993) and in the reed warbler, *Acrocephalus scirpaceus* (Bairlein 2000). Moreover, in garden warblers and reed warblers, the maximum amounts of autumnal fat accumulation are significantly greater in short days than in long days (Bairlein 2000). Interestingly, under natural conditions, late migrants show greater fattening rates than do early migrants (Bairlein 1998a; Schaub and Jenni 2000a, b). Lower food availability and/or shorter days with restricted time for feeding late in the season are thus likely to be significant cues in shaping migratory fattening.

Although the phenomenon of migratory fat accumulation has long been well known, there is still very little known about the nutritional demands and the role of nutrients in the control of migratory body mass gain and about the physiological and biochemical processes involved in migratory fat storage. As food is the principal source of energy for storage, nutritional mechanisms are obviously the most important. However, there are other possible mechanisms which should also be considered (Blem 1980). Here, I primarily focus on summarising those known nutritional adaptations that enable birds to cope with the enormous task of storing enough fuel for their long flights.

Hyperphagia and assimilation efficiency

The extra energy costs involved in accumulating stores for long-distance migration have rarely been investigated. In oystercatchers (*Haemantopus ostralegus*) weighing 540 g, a 1 g change in body mass requires an average extra daily food consumption of approximately 46 kJ (Kersten and Piersma 1987). In garden warblers, migratory body mass gain is associated with a daily net food intake (food metabolised) of 39 kJ/g body mass change (Bairlein 1987b).

An increase in gross daily food intake (amount of food eaten) is a key mechanism in achieving that gain. Reported increases in gross food intake during fattening range from 20% in the white-crowned sparrow, *Zonotrichia leucophrys* (King 1961) to 40% in the dark-bellied brent goose, *Branta b. bernicla* (Bruns and ten Thoren 1990) and the garden warbler (Bairlein 1985).

While this increase in the amount of food eaten fully accounts for the body mass increase in the white-crowned sparrow (King 1961), the white-throated sparrow, *Zonotrichia albicollis* (Odum 1960), the bobolink, *Dolichonyx oryzivorus* (Gifford and Odum 1965), the ortolan bunting, *Emberiza hortulana* (Wallgren 1954), the dark-bellied brent goose, and the whimbrel, *Numenia phaeopus* (Zwarts 1990), it only partly explains the migratory body mass gain in the whitethroat (*Sylvia communis*) and the European robin, *Erithacus rubecula* (Merkel 1958), the yellow wagtail, *Motacilla flava* (Fry et al. 1972), the dickcissel, *Spiza americana* (Zimmermann 1965), the spotted munia, *Lonchura punctulata* (Bhatt and Chandola 1985), and the garden warbler (Bairlein 1985; Hume and Biebach 1996). In these species, hyperphagia is associated with an increase of assimilation efficiency (Bairlein 1999). In garden warblers, for example, the daily body mass gain is associated with a 60% increase in assimilated energy intake, of which 40% is due to an increase in the amount of food eaten (gross food intake), while 20% can be ascribed to an increased assimilation efficiency (Bairlein 1985). The increase in assimilation efficiency is mainly due to changes in the efficiency of fat utilisation.

The mechanisms underlying the observed variation in assimilation efficiency are not clear, and digestive efficiencies are determined by complex interactions of numerous variables (Bairlein 1999). However, there is evidence for adaptive seasonal shifts in dietary nutrient requirements with a preponderance of lipids during premigratory fuelling and thus facilitated lipid uptake (Afik et al. 1997; Lepczyk et al. 2000) which is also reflected in the special role of triglycerides for fuel supply during migration (e.g. Jenni-Eiermann and Jenni 1992; Totzke et al. 1998). A seasonal increase in plasma cholesterol along with fattening (Totzke and Bairlein 1998; Totzke et al. 2000) could reflect an increased need for bile acids to improve the utilisation of fat.

With respect to the seasonal increase in fat assimilation, the recently reported flexibilities in organ size and function deserve attention. In grebes and waders, the size of the digestive tract is reduced prior to migratory flights (Jehl 1997; Piersma 1998; Piersma and Gill 1998; Battley et al. 2000) while garden warblers, incited to a simulated migratory flight, reduced the digestive tract by 63% during migration (Hume and Biebach 1996; Biebach 1998). These organ reductions are viewed as a mechanism to reduce ballast during flight. However, they may also be seen the other way round: it may be that the birds increased their gut size to increase the resorptive capacities resulting in an increased nutrient uptake. In garden warblers, the dry tissue mass of the intestine increased by 25% between a pre-fattening and a fattening group, and this was associated with a significant increase in energy utilisation efficiency (Hume and Biebach 1996).

From the species-specific differences in the extent of changes in food assimilation during migratory fattening, two groups emerge (Berthold 1996): granivorous species with no significant variation, and insectivorous species with pronounced temporal increase in food assimilation efficiency. This difference may reflect the different foraging strategies and associated costs. Granivores often forage in seed-rich habitats where flight energy spent on foraging is reduced and the necessary increase in food intake could easily be achieved by hyperphagia. In insectivores that either forage in the air or fly to food sources, foraging is energetically more costly. Thus, a temporal increase in assimilation efficiency reduces these energetic costs and facilitates fattening.

Seasonal shifts in diet selection – the “frugivory paradox”

Many migrant species show extreme seasonal shifts in diet selection during migratory fattening (Bairlein 1990a). For example, geese feed selectively on a variety of specific plant species during migration, depending upon their particular nutrient requirements. Chaffinches change from an insect diet to a seed diet, and many songbirds switch from a diet consisting almost entirely of insects in spring and summer to high levels of frugivory during autumn. This appears to be contraproductive, as fruits are generally viewed as being of low nutritive, especially of low protein, value, thus preventing the birds from relying on them for extended periods of time, and in particular for migratory fuelling (Berthold 1976b; Izhaki and Safriel 1989; Karasov and Levey 1990; Levey and Cipollini 1999).

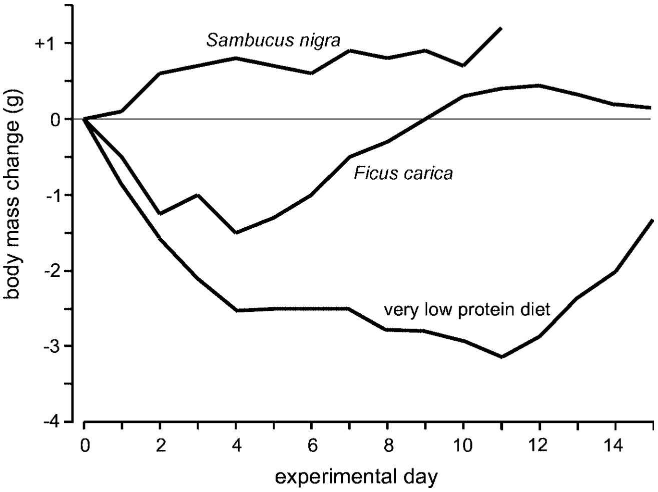

Fig. 2 Body mass of three groups of garden warblers feeding exclusively on black elderberries, figs, or a synthetic diet simulating the very low protein content of fruit (after Bairlein 1987b; Simons and Bairlein 1990). For clarity, error bars have been omitted

Seasonal frugivory in migrants was thought to reflect seasonal changes in the relative availability of insects and fruits. However, seasonal frugivory is primarily the result of changes in food preferences. Even under controlled laboratory conditions with unlimited availability of various food items, the selection of fruits and the extent of frugivory undergo spontaneous seasonal changes (e.g. Berthold 1976b; Wheelwright 1988; Simons and Bairlein 1990; Bairlein 1990a; Whelan and Willson 1994). Moreover, the degree of frugivory during migration and the species-specific preferences for particular fruits often vary irrespective of local fruit abundance in the field (e.g. Kroll 1972; Brensing 1977; Izhaki and Safriel 1985; Willson 1986).

The attempt to unravel the role of fruits in the diets of omnivorous songbirds has been mostly restricted to short-term experiments of only 1–3 days (Berthold 1976b; Izhaki and Safriel 1989). Switching the diet of captive migrants to a pure fruit diet results in a loss of body mass within the first few days, although pronounced differences exist in the effectiveness of different fruits (Fig. 2). These short-term experiments led to the conclusion that these birds are unable to rely exclusively on fruits. However, after this initial decrease, the body mass of the birds recovers even when the birds continue to receive a fruit diet (Fig. 2). Thus, these birds need a few days to adapt to the new feeding situation. After this period they are able to maintain body mass even when kept on a pure fruit diet despite the very low protein and lipid input compared to the intake of insects (Fig. 3). The observed response in body mass is likely to reflect adaptational adjustments to low dietary protein and lipid levels. When garden warblers received a synthetic diet resembling either the low protein content of fruits while keeping the other nutrients constant, they

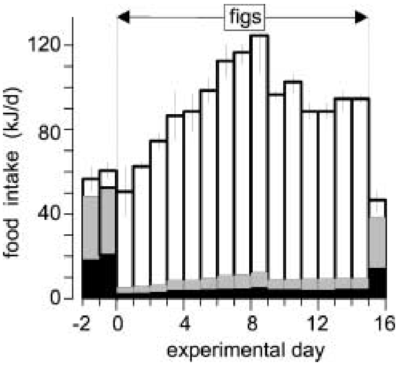

Fig. 3 Average food intake (± SD) of garden warblers feeding exclusively on figs as compared with feeding on an insect-like diet. *Black bars* protein intake, *grey bars* fat intake, *white bars* sugar intake (after Bairlein 1991b)

underwent patterns of body mass changes very similar to those produced by the fruit diet (Fig. 2; Bairlein 1987b). In all cases, adaptation to low nutrient levels was associated with a compensatory increase in food intake (Fig. 3).

Fruit eating and migratory fattening

Captive garden warblers are not only able to maintain their body mass on some pure fruit diets, they can even accumulate as much migratory fat when feeding on certain specific fruits as a control group receiving a insect-like diet (Fig. 4). Interestingly, fruits that did not enable the maintenance of body mass prior to the seasonal phase of migratory fattening, such as alder-buckthorn (*Frangula alnus*), allowed the maintenance of body mass during the period of pre-migratory fattening (F. Bairlein, unpublished). This is strong evidence of seasonal differences in the nutritional requirements or the metabolic machinery of the birds.

Moreover, when the warblers were fed a mixed diet consisting of both insects and fruits on which they are able to accumulate body mass, such as black elderberries or figs, the daily rate of mass gain was even significantly higher than that of warblers fed on a diet of insects alone (Fig. 4). With other fruits, such as red elderberries or alder-buckthorn, such an acceleration in body mass gain did not occur, which again shows substantial differences in the effectiveness of various fruits. This indicates that a yet unidentified "quality" of fruits has to be considered.

These laboratory results are consistent with field data. Several migrant species trapped during autumn stopover had significantly greater body masses and greater daily rates of body mass gain at sites where fruits were available than birds at sites without fruits (Ferns 1975; Thomas 1979; Bairlein 1991a). Parrish (1997) reported that species with greater than one-third of the diet as fruit gained significantly more mass during autumn stopover on Rhode Island than strict insectivores, and that frugivory allowed species to gain mass more efficiently and extensively than exclusive insectivory (Fig. 5).

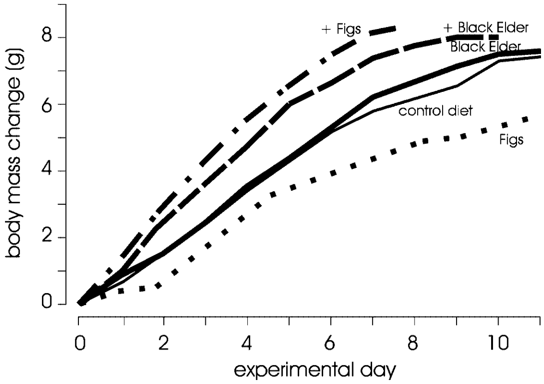

Fig. 4 Mass gain of five groups of garden warblers re-fed with either an insect diet (control diet), a pure fig diet, a pure black elderberry diet, and mixed diets (*broken lines*) consisting of insect diet and figs (+*Figs*) and black elderberries (+*Black Elder*), respectively (sample size is at least 7 birds in each group). For clarity, error bars have been omitted (after Simons and Bairlein 1990; Bairlein and Simons 1995)

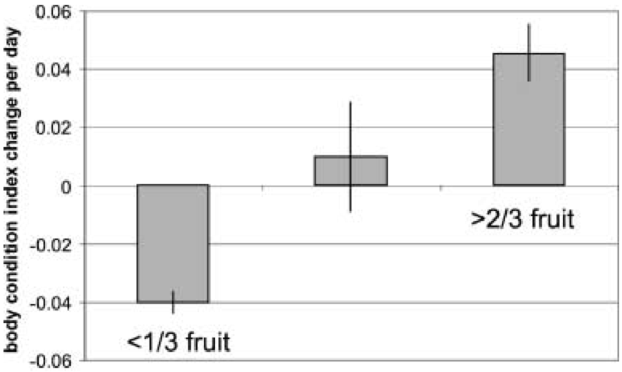

Fig. 5 Relationship between the degree of frugivory and change in energetic condition for autumn stopover migrants on Rhode Island (data from Parrish 1997)

The benefits of fruits

There are two interesting questions: (1) why do some migrants shift their diet from insects to fruits? and (2) how do some fruits accelerate body-mass gain?

Fruits are an "easy prey" (Snow and Snow 1988). Fruits are often abundant locally, and thus the time spent searching for food can be minimised. Owing to their low fibre content, fruits require relatively little mechanical breakdown to make available the nutritious cell contents. Nevertheless, it is often suggested that fruits are a rather poor diet, particularly in terms of protein content (Berthold 1976b; Levey and Cipollini 1999). This appears, however, to be compensated for in fruit-eating migratory songbirds by specific mechanisms of dietary selection.

In dual-choice feeding trials with various berries and fleshy fruits provided ad libitum, the birds which did not have previous experience with the test diets showed well pronounced preferences which were not related to the colour or the size of the fruits. The birds preferred those on which they were able to maintain body mass, while they avoided the berries which did not enable body mass maintenance (Simons and Bairlein 1990; Bairlein 1991b). This illustrates that the birds are able to detect specific nutrient deficiencies and respond quickly and appropriately by effectively regulating the selection and intake of specific nutrients.

Fruits are often rich in sugars. Moreover, the observed compensatory increase in consumption while feeding on fruits results in excessive intake of sugars. However, the sugar content does not appear to be of any significant importance for migratory fattening. High-sugar diets did not promote fat accumulation nor did very low-sugar diets hamper fattening in garden warblers (Bairlein 1998b). Nevertheless, it should be mentioned that selective feeding on aphids, observed in several warbler species during migratory stopovers, is assumed to be related to the high sugar content of these insects (Bibby and Green 1981; Glutz von Blotzheim 1986). Moreover, seasonal modulations of hepatic lipogenic enzymes, such as malic enzyme and fatty acid synthase, as reported in several migrant species (Stevens 1996; Ramenofsky et al. 1999; Egeler et al. 2000), may point on to the use of carbohydrates for migratory fat accumulation in some species.

The role of fats

Among the plant nutrients, dietary lipids seem to play a prominent role. Some of the fruits taken in the wild are high in dietary lipids (Snow and Snow 1988) and, in Mediterranean stopover sites, the seasonal occurrence of many migrant frugivores coincides with a predominance of lipid-rich fruits (Herrera 1984). The dominant role of dietary fat during migratory fattening is also confirmed by feeding-choice experiments involving synthetic diets (Bairlein 1990b). Garden warblers provided with diets which were isocaloric but different in their specific nutrient composition always preferred the lipid-rich diets. Even quite small differences in the lipid content of the diets were detected. This is of particular interest for frugivores, as they appear to be able to select the most lipid-rewarding fruits, irrespective of their generally low lipid content. In addition, eating low-fat diets like fruits is associated with a significant increase in fat assimilation efficiency in garden warblers (Bairlein 1987b), supporting an enhanced uptake of lipids of low-fat diets. Similar data have been obtained by Lepczyk et al. (2000) in American robins (*Turdus migratorius*). They showed a marked increase in the assimilation efficiency of lipids derived from fruits from summer to autumn, which was, however, not associated with a preference for lipid-rich fruits. Rather, they speculated that such an increase in assimilation efficiency of lipids could result from a reduction in intake of lipid-rich fruits as was also reported in other thrushes (Witmer and Van Soest 1998).

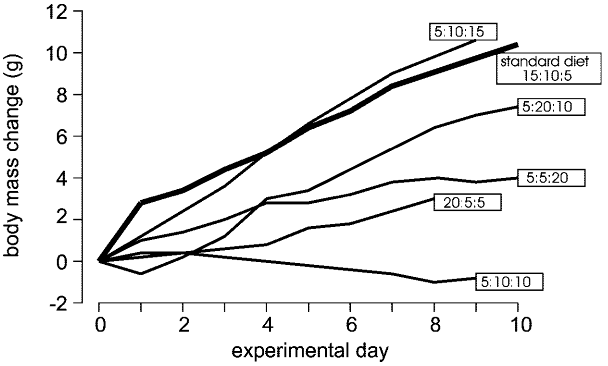

Fig. 6 Body mass changes of various groups of garden warblers fed different diets following food restriction during the seasonal high body mass phase (cf. Fig. 1). The sequence of figures showing the dietary nutrient composition (by wet mass) is %protein, %fat, and %sugar. For clarity, error bars have been omitted (after Bairlein 1998b)

The particular role of dietary lipids in migratory fattening is also revealed by a series of experiments using a synthetic diet (Bairlein 1998b). The nutrient composition of the diet considerably influenced the daily rate of fattening in garden warblers (Fig. 6). A principal components analysis showed that migratory body mass gain in garden warblers is particularly associated with the combined intake of high-energy diets as a consequence of a high fat content (Bairlein 1998b), provided that nitrogen balance is achieved. Highest daily body mass gain was achieved by feeding a protein-reduced diet rich in lipids. A more detailed examination showed that birds feeding on low-protein, high-fat diets had delayed mass recovery for a day, but thereafter the daily rate of body mass gain was even higher than that of the control group. This was associated with an increase in food intake, as a consequence of over-eating in order to meet the protein (nitrogen) balance, which then led to an excessive intake of fat and thus increased body mass gain. High-protein diets, in contrast, retarded body mass recovery. This is likely to be the consequence of a lowered food intake to meet the protein requirements with protein-rich diets and thus insufficient fat uptake. Moreover, nocturnal resting metabolic rate is significantly increased in birds feeding on high-protein diets as compared with low-protein diets (Bairlein and Lehmann, unpublished).

The role of fatty acids

Seasonal frugivory may at least in part be related to the fatty acid composition of plant lipids. Captive garden warblers provided simultaneously with two diets identical in gross lipid content but differing in fatty acid composition exhibited clear preferences for foods rich in C_{18} unsaturated fatty acids (Bairlein 1991b). Feeding the

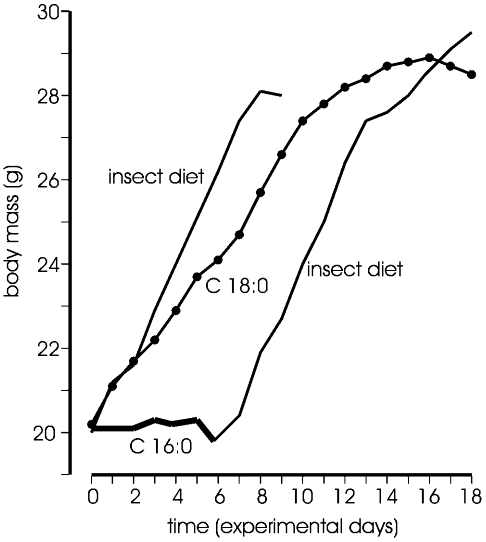

Fig. 7 Body mass gain of three groups of garden warblers fed with either an "insect diet", a diet consisting of pure tristearin lipids (C18:0) or a diet consisting of pure tripalmitin lipids (C16:0) and followed by the insect diet (sample size at least 6 birds in each group). For clarity, error bars have been omitted (after Bairlein and Gwinner 1994)

birds with a pure palmitic acid (C_{16}) food impaired refattening, whereas provisioning of C_{18} fatty acids enabled recovery of body mass (Fig. 7). Whatever the mechanisms are, the preference for C_{18} fatty acid foods and their nutritional effects are particularly interesting in view of the fact that C_{18} fatty acids are predominant in the depot lipids of free-living migrant species (Blem 1976, 1990; Bairlein 1991b). For species which have to achieve high rates of lipid accumulation, it may be very adaptive to incorporate these particular fatty acids directly from their food. As plant lipids are, in general, rich in unsaturated C_{18} fatty acids, seasonal shifts in diet selection and facultative seasonal frugivory may be a specific strategy to promote the accumulation of pre-migratory fat of a particular quality. In non-frugivorous species, selection for phytophagous invertebrate prey that is rich in fatty acids from plants may promote fat deposition. There may also be selective absorption of ingested fatty acids by the intestine. A similar relationship has been found in hibernating mammals where selective feeding on diets rich in unsaturated fatty acids and the uptake of high amounts of unsaturated fatty acids into tissues form part of the preparation for successful hibernation (Geiser 1990). Unsaturated fatty acids, specifically linoleic acid, are potent inhibitors of the binding of thyroid hormone T3 leading to metabolic depression in the rat (Geiser 1990). Chipmunks (*Eutamias amoenus*) on an unsaturated fatty acid diet had lower metabolic rates than those on a saturated diet (Geiser and Kenagy 1987). We found similar effects in fruit-eating garden warblers, where basal metabolic rate was 30% lower on fruit diets. This may reflect a mechanism to maximise the storage of energy despite the low nutrient content in diets such as fruits (Lehmann and Bairlein, unpublished.).

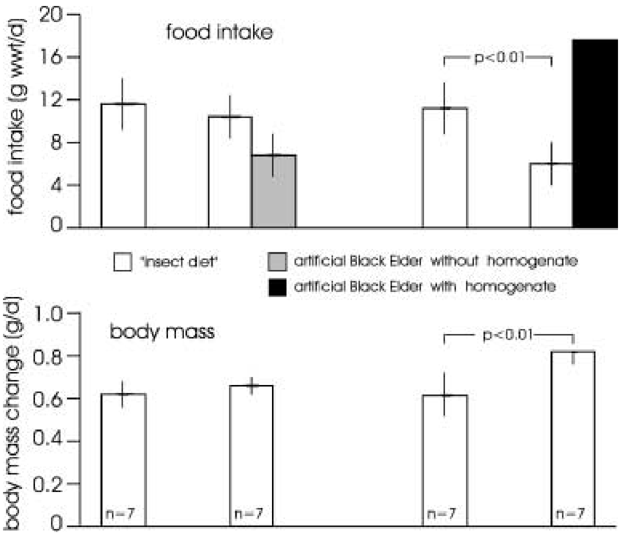

Fig. 8 Average food intake (±SD; *top*) and average body mass changes (± SD; *bottom*) of garden warblers fed either a pure insect diet (*single bar on top*), or a mixed diet consisting of an insect diet and artificial synthetic fruit diets (*paired bars on top*). While feeding a mixed diet comprising an insect diet and simulating the energy and nutrient content of black elderberries but devoid of secondary plant metabolites (*grey bar*) neither food intake nor body mass change varied significantly. Feeding an artificial synthetic fruit diet simulating the actual berries (*black bar*) resulted, however, in changes in diet selection and a significantly greater body mass gain

Secondary plant metabolites

Many fleshy fruits contain considerable amounts of plant secondary metabolites, which are typically seen as having detrimental or even toxic effects on consumers (Robbins 1992). The impact of secondary metabolites on the nutrition of frugivorous birds has been largely overlooked, or is controversial (Levey and Cipollini 1999). Many fruits regularly taken by frugivores contain high levels of secondary compounds. Garden warblers or blackcaps (*Sylvia atricapilla*), for example, eating black elderberries, which contain approximately 5% of tannins per dry weight, consume around 800 mg of tannins per day (Bairlein 1996). The mechanisms by which these frugivores deal with these amounts of possibly detrimental chemicals have not yet been explored. Fruit-eating birds may possess mechanisms to detoxify or to tolerate these chemicals or to render themselves immune to their effects (Bairlein 1996; Levey and Cipollini 1999).

However, there is evidence that some fruits may be taken because of their secondary compounds. Garden warblers fed an artificial synthetic fruit diet simulating the energy and nutrient content of black elderberries but devoid of secondary plant metabolites did not vary food intake nor body mass (Fig. 8). In contrast, conspecifics fed on a diet supplemented with small amounts of a homogenate of black elderberries containing the secondary metabolites, exhibited an almost 50% increase in daily food intake and a continuous daily increase in body mass

(Fig. 8). In dual-choice trials, they preferred the diet supplemented with the homogenate (Fig. 8). Whatever the mechanisms are, these data suggest that a yet unidentified particular "quality" of the fruits has to be considered when evaluating the role of fruits in the diets of consumers that is beyond the role of the nutrients. Interestingly, differences emerged even between closely related fruit-eating species. While captive garden warblers significantly lost body mass when fed privet, the closely related blackcaps did not (Bairlein 1990a and unpublished.). Blackcaps have been reported eating privet in the wild while garden warblers have not (Snow and Snow 1988). The difference in nutritional consequences of privet in both species may be due to a missing coevolution of garden warblers and privet present in blackcaps. Owing to earlier migration in autumn and later arrival in spring, the seasonal occurrence of garden warblers does not coincide with the fruiting periods of privet, while blackcaps naturally coincide with the availability of ripe privet.

Nutrition and metabolism

Even less than about the nutritional mechanisms is known about how food intake and selection are controlled and how the nutritional energy is metabolised and translated into body stores. Blem (1980) has already proposed that a decreased metabolic rate may facilitate migratory fattening. The combination of an increased food intake with a decrease in total energy expenditure dramatically increases lipid storage in several mammalian hibernators (Geiser 1990). In birds, however, so far there is only little evidence (Berthold 1996). Data on seasonal changes in the basal metabolic rate in relation to migration are scant and contradictory. Carpenter and Hixon (1988) and Hiebert (1993) speculated that migrant hummingbirds use torpor to conserve fat stores for later use when migrating. However, it may also be a means to increase the daily net gain of fuel stores. Metabolic rates of several waders were lower at their tropical wintering grounds (Klaassen et al. 1990; Bairlein 1993; Piersma et al. 1995; Lindström 1997), which may support fattening for spring migration. However, in garden warblers and blackcaps kept under constant conditions, no significant changes in basal metabolic rate were found prior to and during fattening (Lehmann and Bairlein, unpublished). In red knots (*Calidris canutus*), basal metabolic rate was even higher at times of high body mass (Weber and Piersma 1996).

Fattening in migratory birds: a model for studies of human obesity?

Hyperphagia and migratory fattening come across with significant metabolic changes as indicated by simultaneous seasonal variations of several plasma metabolite levels (Bairlein 1983; Bairlein and Totzke 1992; Singh et al. 1993; Totzke and Bairlein 1998; Williams et al. 1999; Hintz 2000) and tissue enzyme activities (Marsh 1984; Lundgren and Kiesling 1985; Ramenofsky 1990). In particular, increased plasma glucose and lipid levels in fat birds are similar to mammalian obesity, which often results in the so-called metabolic syndrome. Likewise, garden warblers also show lower glucose utilisation rates in the fat condition and after fasting (Totzke et al. 1998). This may be due to the inhibition of glucose oxidation by high circulating levels of fatty acids. The mutual inhibition of glucose and fatty acid oxidation [as first described by Randle et al. (1963) in the so-called glucose–fatty acid cycle] may explain the birds' preference for lipid rather than carbohydrate diets after the metabolism and the enzyme machinery has adopted to the high lipid oxidation capacity (Marsh 1984; Lundgren and Kiesling 1985) required during migration. The glucose–fatty acid cycle may be further involved in the spontaneous rhythmic body mass variations during the high-fat phase observed in garden warblers kept under constant conditions (Bairlein 1986). The period length of this rhythm matches no natural rhythm but is influenced by the fat and sugar content of the diet.

As in the human metabolic syndrome, pancreatic hormones and, in particular, insulin resistance are also likely to be involved in the metabolic changes during migratory fat accumulation (Totzke et al. 1997, 1998, 1999; Hintz 2000). In general, pancreatic hormones appear to have similar effects in birds and mammals (e.g. Hazelwood 2000); however, as indicated by the higher glucose levels and glucagon:insulin ratios, their functional role in birds appear to be different (Totzke et al. 1997). In particular, this still needs to be elaborated in migratory species with distinct body mass variation.

The recently discovered fat-regulating hormone, leptin, with respect to its proposed role in mammals (Friedman 2000; Reidy and Weber 2000) should warrant particular interest. Although found in birds (Ashwell et al. 1999; Denbow et al. 2000), its role in the regulation of migratory fattening is unknown. Seasonal changes in circulating leptin concentration, coupled with decreases in leptin receptor density, may promote the accumulation of migratory fat (Reidy and Weber 2000). Seasonal changes in leptin sensitivity have been suggested as playing a significant role in the regulation of seasonal body mass in some hibernators (Klingenspor et al. 2000).

Even less is known about the role of neuropeptides discussed in mammalian obesity (Schwartz et al. 2000) with respect to fattening birds. Richardson et al. (1995) reported increased sensitivity to neuropeptide Y in white-crowned sparrows kept in long photoperiods, resulting in increased food intake and body mass gain, but it remains to be discovered whether seasonally altered sensitivity to NPY underlies pre-migratory fattening. Finally, the newly discovered nuclear receptors PPARs (peroxisome proliferator-activated receptors), in particular the isotype PPARγ, should focus interest. It is mainly expressed in the adipose tissue, it promotes fat storage and insulin sensitivity in mammals, and it is viewed as playing a key role in adipogenesis (Auwerx 1999; Kersten et al. 2000).

The bird's metabolic situation during migratory fattening shows obvious similarities to the human metabolic syndrome. While this has to be considered as pathological in humans, the spontaneous accumulation of fat in migratory birds is a regular seasonal event adapting to the requirements of migration. However, it is reversed even in captivity when birds are prevented from expending these stores by long-distance flights and its simultaneous metabolic changes appear to be well regulated. Thus, the fat accumulation in migratory birds may provide an exciting animal model for studying the nutritional and biochemical regulation of body mass and obesity.

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