Chapter 3

Fuel Deposition Rate and Energy Efficiency of Stopovers

Abstract In this chapter I review the methods of estimating the fuel deposition rate (FDR) of stopover migrants. These methods are based either on body mass change in the birds captured at least twice, or on body mass relationship with the time of day in single captures, or on analysis of metabolites in blood plasma. There is no perfect method; every approach has its benefits and pitfalls. The empirical values of the FDR reported in the literature are reviewed, and various factors that influence the FDR during migratory stopovers are discussed. Very often the FDR does not remain constant throughout stopover: it is low or even negative during 1–2 days after arrival but subsequently increases. It may also drop again towards the end of stopover. The ecological and behavioural causes and implications are discussed.

3.1 Energy Stores of Migrants

As mentioned in the Introduction, energy stores of migrating birds include not only adipose tissue but also some proteins (Piersma 1990; Lindström and Piersma 1993). In the thrush nightingale *Luscinia luscinia* fat made up 80–82% of stores, water, 12–14% and protein, 5–6% in mass (Klaassen and Biebach 1994; Klaassen et al. 1997). However, it should be mentioned that in first-autumn sedge warblers fat constituted 100% of stores above the lean body mass of 11.55 g (n = 20; Baggot 1986). It is generally assumed that birds extract ca. 5–10% of energy for the sustained migratory flight from protein (Jenni and Jenni-Eiermann 1998). It seems to be a small proportion, but the point is that energy density of wet protein is eight times lower than that of adipose tissue (Jenni and Jenni-Eiermann 1998). If this proportion is correct, protein should make up between 30% (if is the source of 5% of energy) and 47% (the 10% of energy case) of fuel stores in mass. Thus, it may be that in reality, a smaller proportion of energy is extracted from protein.

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Apparently the amount of energy derived from protein varies between the species of songbirds.

It has been suggested that long-distance migrants rely on protein to a smaller extent than short- to medium-distance migrants do (Jenni-Eiermann and Jenni 1991) and that purely insectivorous passerines burn more protein than species that consume large quantities of fruit rich in carbohydrates (Gannes 2001). It has also been reported that elevated blood concentrations of urea, indicative of increased protein oxidation, were typical of emaciated songbirds captured in the Sahara during autumn passage, i.e. that burning protein might be the last resort of individuals that have run out of lipid fuel (Bairlein and Totzke 1992).

Anyway, the potential flight range is greatly dependent on the proportion of protein in fuel stores (Jenni-Eiermann and Jenni 2003). Unlike lipids or carbohydrates, protein is stored as functioning tissue, therefore migrating birds that extract energy by burning protein have to get it from the breast muscle, gut, leg muscles etc. (Schwilch et al. 2002; Bauchinger and Biebach 2005).

3.2 Methods of Estimating Fuel Deposition Rate

3.2.1 FDR Estimates From Recaptures

As is the case with the stopover duration, estimating FDR has several methodological issues. There are two main methods to estimate it: on the basis of the mass change in the birds captured at least twice, and based on the mean mass change of samples of the birds captured during the day.

In the former case the analysis is aimed at estimating the daily FDR, measured in g day^{-1}. One of the difficulties is that if captures are made during the whole day, the body mass of individuals generally increases towards dusk as compared with dawn, because they forage (Klein et al. 1971; Dolnik 1975). The time of the first and the last capture seriously influence the body mass measurements. Attempts have been made to circumvent this problem by restricting trapping (or analysis) to morning hours. Unfortunately, this solution is not a good one, because mass is gained at the greatest rate before noon (when the morning activity and foraging peak takes place), and varies to a smaller degree in the afternoon [our data, see also Bardin (1998) on winter fuel stores in great tits *Parus major*].

Sometimes body mass is corrected for capture time. Body mass is standardised, usually by linear regression of body mass on time of the day, and then body mass change between the first and the last capture is calculated (Moore and Kerlinger 1987; Moore and Wang 1991; Chernetsov 1998).

The most correct method of estimating FDR from recaptures is based on multiple regression models (Schaub and Jenni 2000). The idea is that by stepwise multiple regression two coefficients are estimated, the mass gain rate during the day (a) and fuel deposited rate (b) after correcting for mass loss during the night

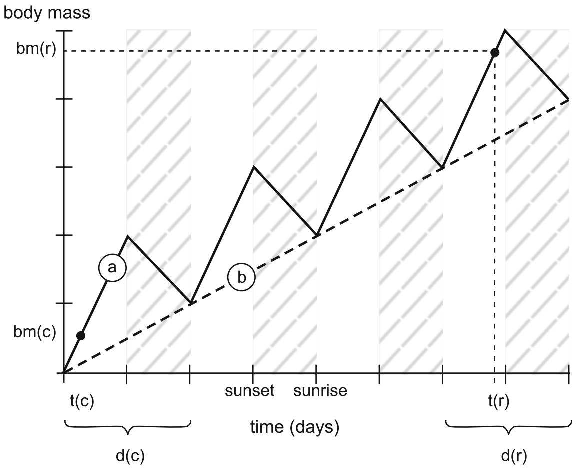

Fig. 3.1 A model of the body mass development of a migrant at stopover over several days (nights are shaded; altered from Schaub and Jenni 2000a). Explanations in the text

(Fig. 3.1). The initial capture and marking date [d(c)], time [t(c)] and body mass [bm(c)] are known for each individual. The respective parameters are also known for the recaptures [d(r), t(r), bm(r)]. This makes it possible to calculate body mass change during stopover from the equation:

$$\mathrm{bm(r)} - \mathrm{bm(c)} = a\,[\mathrm{daylength} - \mathrm{t(c)}] + b\,(\mathrm{d(r)} - \mathrm{d(c)} - a\,[\mathrm{daylength} - \mathrm{t(r)}], \tag{3.1}$$

which is equivalent to

$$\begin{aligned} \mathrm{bm(r)} - \mathrm{bm(c)} &= a\,[\mathrm{t(r)} - \mathrm{t(c)}] + b\,[\mathrm{d(r)} - \mathrm{d(c)}], \text{ or} \\ \mathrm{bm(r)} - \mathrm{bm(c)} &= a\,\Delta\mathrm{time} + b\,\Delta\mathrm{date} \end{aligned} \tag{3.2}$$

Thus, the dependent variable is mass change between the last and the first capture, and the independent variables (predictors) are the difference between the time of the last and the first capture (in hours) and the number of the days elapsed. When $\Delta\mathrm{time} = 1$ h, a is hourly mass change rate. When $\Delta\mathrm{date} = 1$ day, b is body mass change per day, i.e. FDR in g day^{-1}.

This method assumes that the body mass of stopover migrants linearly increases during the daytime and linearly decreases during the night (Fig. 3.1). In reality, deviations from the linear relationship between body mass and time of the day are usually small and not statistically significant (Schaub and Jenni 2000; Chernetsov and Titov 2001). An important advantage of this method is that it allows inclusion of additional parameters into the model and testing their significance. In the model, intercept is chosen to be equal to zero, as with zero time change mass change is obviously zero.

The disadvantage of this method is its dependence on recaptures. If the recapture probability varies between different cohorts of birds (e.g. because of their different mobility), artefacts may arise. Let us assume that all birds of some species intend to depart from the stopover site when they reach the same optimal departure body mass (or fuel load) and that both fat and lean individuals have the same mean FDR. Birds initially captured with a low body mass need relatively much time to reach the threshold body mass, during which individuals with both high and low FDR can be captured. Thus, for the initially lean birds we obtain a reliable mean FDR estimate. However, individuals with initially high body mass (close to the threshold) that gain mass slowly have a high probability of capture. But initially fat birds with high FDR quickly reach the threshold body mass and have a low probability of recapture during their brief stopover period. Therefore the mean FDR of fat birds is underestimated, and the overall mean FDR estimate is biased low, too. Moreover, it appears that FDR is inversely related to the initial body mass which is not actually true. Indeed, the inverse relationships between FDR and initial body mass (or fuel load) have been reported many times (Loria and Moore 1990; Fransson 1998; Schaub and Jenni 2000; Chernetsov 2001; Chernetsov and Titov 2001). It is impossible to decide whether this effect is an artefact on the basis of recaptures.

Last but not least, the estimates of FDR by captures and recaptures is by definition only possible for individuals that were captured at least twice. The assumption that these birds are a representative sample of all migrants at stopover is at least not self-evident and in most cases probably incorrect (Chap. 6).

3.2.2 FDR Estimates From Mass Change of First Captures

Another method of estimating FDR of migrants at stopovers is based on analysing the hourly trend of the mean mass of the first captures (Yablonkevich and Shapoval 1987; Winker et al. 1992; Dunn 2000). The resulting estimates are then not the daily, but the hourly mass change rate. Instead of the body mass change, the condition index change may be used, i.e. the change in size-corrected body mass (Labocha and Hayes 2012). As the proxy of structural size, wing length (Winker 1995; Dunn 2002; Ktitorov et al. 2008; Johnson and Winker 2008; Seewagen and Slayton 2008), or wing length raised to the third power (Dunn 2001) may be used. If the values obtained from different species are compared, FDR is expressed as percentage of the lean body mass (Lindström 1991, 2003). Hourly mass change rate may be compared with hourly nocturnal loss rate which is sometimes assumed to be 4.5% of lean body mass (Winker et al. 1992). However, estimates of nocturnal body mass loss rate based on the allometric equations may be more accurate (Dunn 2001). As an example of field data on body mass loss the data of Zimin (2003) on European robins may be given: during autumn migration the birds were losing on average 1.42 g per night (9.5%) under outdoor temperatures, with the average hourly rate of 1.2%. In chaffinches *Fringilla coelebs* in migratory disposition under outdoor temperature nocturnal mass loss was 0.103 g h^{-1} (SE = 0.011; Dolnik and Gavrilov 1973a), i.e. 0.5% per hour assuming the lean body mass of 20.0 g (Dolnik and Gavrilov 1973b). The daily mass gain should at least balance the nocturnal mass loss; otherwise the migrant will be losing mass instead of gaining it.

The estimates obtained by this method may be mainly used for comparing FDR values between different sites (Dunn 2002; Ktitorov et al. 2008). This data is difficult to use for the absolute estimates of mass change rate across several days, because estimates of nocturnal mass loss from allometric equations are rather rough and do not include thermoregulation costs that may differ considerably with calendar dates, geographic regions or even individually (Zimin 2003).

An important advantage of estimating mass change rate from single captures is that this approach does not exclude individuals that are only trapped once. Such birds are a great majority in any trapping project. This approach may only be used if all migratory flights are only performed at night: all the birds must arrive before the trapping starts. Otherwise individuals that arrive later during the day may be leaner (having depleted their fuel stores) than those captured early in the morning. Such situations may occur on offshore islands or on the coast where the migrants arrive after crossing large water bodies (Moore and Aborn 1996). Under such conditions even species that are normally pure nocturnal migrants may be forced to continue their flights after sunrise.

3.2.3 FDR Estimates From Blood Metabolites

The estimates based on multiple captures are limited by the fact that to be included, any bird should be captured at least twice. The method based on the hourly change of the mean body mass makes a non-obvious assumption that the diel rhythm of activity is the same in stopover migrants with different fuel loads. It has been shown that at least in some songbird migrants this is not what happens (Yablonkevich et al. 1985; Brensing 1989; Titov 1999b).

An attempt to circumvent these problems has been made by estimating the fuel deposition rate in migrants captured only once from concentrations of certain metabolites in blood plasma (mainly triglycerides, free glycerol and β-hydroxybutyrate). Plasma levels of triglycerides are positively, and those of β-hydroxybutyrate negatively correlated with body mass changes during several hours preceding sampling (Jenni-Eiermann and Jenni 1994; Williams et al. 1999; Jenni and Schwilch 2001; Cerasale and Guglielmo 2006). Most triglycerides originate from diet, either directly, or through synthesis in the liver; therefore high triglyceride concentrations indicate lipid transport to the peripheral tissues, i.e. fat deposition. β-hydroxybutyrate is a ketone body synthesized from fatty free acids which replaces glucose under the negative energy balance. Its high concentration in the plasma indicates the catabolism of fat. Therefore, high concentrations of these products are indicative of lipogenesis or catabolism of lipids in the organism. The plasma concentration of the third important metabolite, free glycerol, increases during lipid catabolism (Stevens 2004).

The study of the fuel deposition rate by analysing plasma concentrations of certain metabolites that indicate processes of lipid synthesis or catabolism is a promising avenue of research. Its obvious benefit is that a bird needs to be captured only once, so that the handling effect during the previous capture is absent. On the other hand, the results of analysis make it possible to determine processes that prevailed during the several hours preceding blood sampling. As FDR may seriously change during the stopover period (see below, Sect. 3.5), the data may not be representative of the whole duration of the stay. Moreover, the data obtained by this method allows comparisons between species, seasons, study sites (Schaub and Jenni 2001; Gannes 2001) or habitats (Leist 2007), but it is not straightforward to obtain absolute FDR values (in grams per hour or per day) from the plasma concentrations of metabolites. Attempted have been made to predict the body mass change rate from plasma metabolite concentrations in Eurasian reed warblers (Jenni and Schwilch 2001). However, at least 50% of body mass change variation remained unexplained, and it remained unclear how universal was the calibration equation obtained. It is not impossible that every songbird species will require its own species-specific calibration coefficient, which would make using this method for obtaining absolute estimates of FDR rather problematic.

3.3 Empirical FDR Values

3.3.1 The Mean and Maximum Values Observed

The FDR of songbird migrants during stopovers is usually ca. 1–3% of lean body mass per day (Lindström 2003). The median value for 31 species of passerine migrants was 2.4% (Biebach 1996). In small birds FDR (as the percentage of their lean body mass) was higher than in large ones. The maximum values of the mean FDR known for a species were related to the body mass as $\mathrm{FDR}_{\max} = 2.17\ \mathrm{m}^{-0.34}$ ($r^2 = 0.54$; $p < 0.001$; 95% confidence interval of the exponential coefficient -0.44 to (-0.23); Lindström 2003). The highest FDR values reported in passerines were 12.4% of lean body mass per day in sedge warblers (Gladwin 1963), 12.5% in garden warblers and 13.0% in Eurasian reed warblers (N. Baccetti in Lindström 2003). It remains unclear how these values were obtained. They are probably not the net daily FDR (*b* coefficient in Fig. 3.1), but the mass increase during the day (*a* coefficient). Similarly high values (11.2–13.6% of lean body mass per day) were obtained for the grey catbird *Dumetella carolinensis*, northern waterthrush, red-eyed vireo, and several *Empidonax* flycatchers during the autumn passage in southern Belize (Johnson and Winker 2008). However, these values may also be biased high due to the underestimated values of nocturnal body mass loss in that study.

The physiological limit of mass accumulation rate when food is provided *ad libitum* is even higher: some sedge warblers increased their body mass by more than 20% of their lean body mass per day in a field experiment with supplementary food provision (Bayly 2006). Apparently, the migrating passerines never or nearly never reach such FDR values in the wild. Most field data yield much lower values. It should be however kept in mind that most empirical values are more or less biased low.

Data for 48 species of songbirds captured on the shore of Lake Erie in North America based on the increase of the mean mass of the first captures during the day give the mean value of 0.50% of lean body mass per hour during spring passage and 0.61% in autumn (Dunn 2001). The data for 14 species at 15 sites in southern Canada yield 0.40% of lean body mass per hour in spring and 0.53% in autumn (Dunn 2002). These values are very close to FDR values of European robins based on recaptures (see below).

3.3.2 Case Study: The European Robin on the Courish Spit

A detailed analysis of FDR at stopover and factors that influence it was made by Tsvey (2008) in a case study of European robins on the Courish Spit in the Eastern Baltic. In order to estimate the FDR during the day (body mass increase rate during the day, g h^{-1}) and the net FDR during the stopover (g day^{-1}) the author selected 895 capture histories of European robins (177 in spring and 718 in autumn) trapped in 1994–2003 on Cape Rossitten on the Courish Spit. In spring, captures occurred on 27 March–15 May and involved 33 adults and 144 second-year birds. In autumn, 40 adults and 678 hatching-year birds were captured between 1 September and 6 November. All the adults had their post-breeding moult completed; 55 first-autumn robins were at final stages of juvenile moult.

The capture histories selected for analysis met the following four conditions. First, only those capture histories of birds were included which had been initially captured during the first or the second day of a wave of arrivals. The first capture at the beginning of a wave strongly suggested that the bird had been marked soon after arrival (Sect. 2.1, see also Titov and Chernetsov 1999b; Chernetsov and Titov 2000). The initial body mass of such birds is more or less representative of arrival fuel stores.

Second, only those cases were included in which the minimum stopover duration (time elapsed between the first and the last capture) did not exceed 12 days in spring and 17 days in autumn. These values were selected on the basis of frequency distribution of stopover durations of European robins when the capture histories met the first criterion, and on the basis of radio-tracking data (Sect. 2.3) and of recaptures in high mist-nets.

Third, to reduce the bias caused by handling effect, only those cases were considered when at least two days elapsed between the initial marking and the first recapture. Finally, in the cases of multiple recaptures only the body masses at the first and the last capture were included. If multiple captures occurred during the last and penultimate day of proven stay, only the first of these captures was considered. For example, if a robin was captured three times on 18 September and once more on 19 September, the first capture on 18 September was analysed. This was done to minimise the possible effect of handling stress.

By following these selection criteria, Tsvey (2008) analysed the data that referred to birds that stopped over for three and more days, i.e. were ‘feeders’, not 'flyers' sensu Rappole and Warner (1976); and were captured soon after arrival. The author included eight potential predictors of the rate of body mass change into the multiple regression model. These predictors were (1) season (spring vs. autumn); (2) progress of season; (3) age of birds (first- or second-year vs. adults); (4) condition index at the first capture, calculated as CI = body mass · wing length$^{-0.852}$, where body mass is standardised for 8 a.m., and exponent follows Titov and Chernetsov (1999a); (5) wing length as size proxy; (6) number of European robins at the study site during stopover of each individual birds as a proxy of density of conspecifics; (7) air temperature at midday; (8) year.

The best model selected by backward stepwise elimination and including both spring and autumn data explained 26% of FDR variance ($r^2 = 0.26$, $F_{3,891} = 103.1$, $p < 0.0001$, $n = 895$) and resulted in the estimate of 0.084 g h^{-1}. It makes 0.57% of lean body mass of an average European robin with a wing length of 72 mm. It is noteworthy that when large samples are analysed, the estimates obtained by different methods are very similar. The analysis of the first captures across time of the day on Cape Rossitten in 1994–2001 suggested a body mass increase of 0.0804 g·h^{-1} (body mass = 15.15 + 0.0804 h, $r^2 = 0.072$, $n = 46{,}730$, $p < 0.01$), i.e. 0.5% per hour. Captures of European robins in elevated mist-nets after one-day stopovers yielded FDR estimate of 0.0823 g h^{-1} (SD = 0.04, n = 24; Bulyuk and Tsvey 2006). The latter value is based on two captures of individual birds.

The net FDR (coefficient *b*) after correction for the time of the day was 0.064 g day^{-1} for autumn migration (0.44% of lean body mass) and only 0.007 g day^{-1} in spring (Tsvey 2008). This means that in spring, the FDR of European robins on the Courish Spit was very close to zero. Estimates for the autumn passage are close to the figures reported from Helgoland in the North Sea, based on recaptures: 0.04–0.11 g day^{-1}, depending on the progress of season (Ottich and Dierschke 2003).

During spring passage, both mass increase during the day and net energy efficiency of stopover were inversely related to the initial condition index (Table 3.1). Lean European robins (with the mean condition index of 0.385, i.e. mean body mass of 14.72 g) increased their body mass by 0.09 g h^{-1}, whereas fat robins (with the mean condition index of 0.427, i.e. mean body mass of 16.33 g), by 0.06 g h^{-1}. Lean individuals gained mass by 0.065 g day^{-1}, and their fat conspecifics lost mass by 0.11 g day^{-1}. In 2001 FDR was significantly (by 0.26 g day^{-1}) higher than in other years, and even fat European robins increased their body mass at stopovers on the Courish Spit (on average by 0.15 g day^{-1}).

In autumn, body mass gain during the day was positively related to the progress of the season (Table 3.2), i.e. foraging efficiency increased from 0.083 g h^{-1} on 1 September to 0.104 g h^{-1} on 31 October. The energy efficiency of stopovers was significantly related to their initial fuel stores and the number of birds present at stopover (a proxy of competition). In 1995 FDR was significantly lower than in the remaining years, other factors being held equal (Table 3.2). Lean European robins increased their body mass on average by 0.13 g day^{-1}, whereas the body mass of

Table 3.1 Multiple regression model explaining the rate of the body mass change in European robins on the Courish Spit during spring passage (from Tsvey 2008)

Parameter	Regression coefficient	SE	Significance
Δtime	0.370	0.134	$p < 0.0001$
Δtime·CI	−0.727	0.330	$p < 0.05$
Δdate	1.595	0.212	$p < 0.0001$
Δdate·CI	−3.988	0.527	$p < 0.0001$
Δdate·year 2001	0.255	0.079	$p < 0.001$

$R^2 = 0.46$; $F_{5,172} = 28.9$, $p < 0.0001$, $n = 177$. Δtime is the hourly mass change rate; Δdate is the daily mass change rate taking account of nocturnal mass loss; CI is condition index (size-corrected body mass) at the first capture

Table 3.2 Multiple regression model explaining the rate of body mass change in European robins on the Courish Spit during autumn passage (from Tsvey 2008)

Parameter	Regression coefficient	SE	Significance
Δtime·season progress	0.00034	0.00003	$p < 0.0001$
Δdate	1.277	0.100	$p < 0.0001$
Δdate·CI	−2.878	0.245	$p < 0.0001$
Δdate·number	−0.0003	0.00008	$p < 0.0001$
Δdate·year 1995	−0.0093	0.018	$p < 0.0001$

$R^2 = 0.41$; $F_{5,713} = 100.5$, $p < 0.0001$, $n = 718$. Δtime is the hourly mass change rate; Δdate is the daily mass change rate taking account of nocturnal mass loss; CI is condition index (size-corrected body mass) at the first capture; number is the mean daily trapping figure during the migratory stopover of a particular bird

fat birds practically did not change: their FDR was 0.011 g day^{-1} (the mean number of conspecifics at the stopover site was 122 individuals). In 1995, fat robins increased their body mass by 0.04 g day^{-1}, lean birds lost body mass by 0.08 g day^{-1}.

3.3.3 FDR Estimates From Blood Metabolites Analysis

A broad-scale field study of fuel deposition rate by analysing blood metabolites in the Eurasian reed warbler, sedge warbler, garden warbler and pied flycatcher was performed by Schaub and Jenni (2001). The authors reduced two parameters, plasma levels of triglycerides and *β*-hydroxybutyrate, to the single 'fattening index' by principal component analysis. They translated the values of this fattening index into body mass change from sunrise to sunset (i.e. coefficient *a*) for Eurasian reed warblers using the calibration equation developed by Jenni and Schwilch (2001). The results varied between 0.190 g over the daylight hours in Ebro delta (Spain) and 1.028 g in Oued Moulouya (Morocco, just before crossing the Sahara in autumn). These estimates seem to be the realistic ones.

3.4 Factors that Influence FDR

3.4.1 Effect of Initial Fuel Stores

The factor that nearly always significantly negatively influences FDR of migrants is their energy condition (condition index) at the first capture (Loria and Moore 1990; Fransson 1998; Schaub and Jenni 2000; Chernetsov 2001, 2003, 2010; Bayly and Rumsey 2007; Chernetsov et al. 2007; Tsvey 2008; Panov and Chernetsov 2010). It has already been mentioned (Sect. 3.2.1) that it may be an artefact. It is however worth noting that mobility of fat and lean European robins in the first two days of stopover on the Courish Spit did not differ (Sect. 6.5), so that the capture probability should not necessarily be fuel load-related. The capture probability of several species of long-distance migrants in an oasis in the western Sahara has also been shown to be independent of fuel load (Salewski and Schaub 2007). Under experimental conditions caged fat European robins lose body mass during the first week after capture, whereas lean birds start to gain body mass immediately after being taken into captivity (Tsvey 2008). Song thrushes *Turdus philomelos* do the same (Chernetsov, unpubl.). Therefore it cannot be ruled out that at least in some cases the inverse relationship between the initial body mass and FDR is not due to methodological issues but is a real phenomenon. Migrants with high fuel stores probably invest more time and effort into caring about their safety from predators (Fransson and Weber 1997) and spend less time in habitats rich in food but more open and thus providing less protection from predators (Moore 1994; Dierschke 2003; Sapir et al. 2004; Wang and Moore 2005).

Only a single study reported a positive relationship between current body mass and FDR in stopover migrants (Schaub and Jenni 2001). In this study FDR was estimated not from recaptures but from blood metabolite analysis (Sects. 3.2.3, 3.3.3). In three species out of four included in the analysis (in the Eurasian reed warbler, sedge and garden warblers) the lipid synthesis rate was positively correlated with body mass. This study was free from the potential methodological issues discussed in Sect. 3.2.1, when the FDR estimates of initially fat birds may be biased low. On the other hand, it cannot be ruled out that the amount of stored lipids also influences the level of triglycerides, free glycerol and β-hydroxybutyrate, apart from the rate of lipid catabolism.

3.4.2 Progress of Season

Another factor that is often included into multiple regression models as a significant predictor of FDR is progress of season. In the sedge warbler and Eurasian reed warbler across most of Europe (Schaub and Jenni 2000; Balança and Schaub 2005), in the blackcap on the Courish Spit (Chernetsov and Titov 2001), in the whitethroat in Sweden (Fransson 1998), in the European robin on the Courish Spit

(Tsvey 2008) and on Helgoland (Ottich and Dierschke 2003) the energy efficiency of stopovers increased towards the end of autumn passage. However, the FDR of garden warblers across Europe (Schaub and Jenni 2000) and bluethroats in northern Karelia (Panov and Chernetsov 2010) was not related to progress of season. Increasing FDR in the end of autumn allows migrants to deposit greater fuel stores even without increasing stopover duration. It makes it possible to make longer flights and thus to increase the overall speed of migration.

The adaptive value of high FDR at the end of the autumn migratory season is obvious. Delayed individuals need to leave quickly the areas where the weather and foraging opportunities rapidly deteriorate or at least become unpredictable. Indeed, the speed of migration is known to increase towards the end of the season (Ellegren 1993; Fransson 1995; Bensch and Nielsen 1999). Furthermore, it may be essential for a number of species to arrive early or at least not too late to wintering areas, just like it is important to arrive first in spring (Kokko 1999). It concerns species like the pied flycatcher or European robin that are territorial in winter quarters (von Stünzner-Karbe 1996; Cuadrado 1997; Salewski 1999; Tellería and Péres-Tris 2004) and like *Acrocephalus* warblers for whom early arrival at Africa may make it possible to undergo moult at the beginning of winter (Bensch et al. 1991).

It is less clear how the birds increase their fuel deposition rate at the end of the autumn migratory season. It is usually assumed that food availability for the insectivorous songbirds declines at the end of autumn. This is not so for the European robin, whose prey availability increases towards the end of the autumn migratory season in the Eastern Baltic, because hibernating invertebrates gather in the ground layer late in autumn and become more available for foraging robins (Titov 2000). It is worth noting that in this species the gain rate of body mass during the day (coefficient *a*) increases in late autumn, but the net FDR (coefficient *b*) does not (Table 3.2). How *Acrocephalus* warblers manage to increase their FDR in late autumn (Schaub and Jenni 2000, 2001; Balança and Schaub 2005), if they mainly consume highly seasonal plum aphids (Bibby and Green 1981; Chernetsov and Manukyan 1999a, b, 2000) and their prey availability does decline in late autumn, is more difficult to understand. Endogenously controlled increase in FDR towards the end of the autumn migratory period has been recorded in captive long-distance migrants under the laboratory conditions (Bairlein 2000). It seems that in many cases migrating songbirds do not gain mass at the maximum possible rate, and they are able to increase FDR when necessary, e.g. when delayed in northern areas in late autumn, or before crossing an ecological barrier.

3.4.3 Competition

An inverse relationship between the number of conspecifics present at the stopover site and FDR was found during autumn passage in goldcrests *Regulus regulus* in Sweden (Hansson and Pettersson 1989), in the Wilson's warbler *Wilsonia pusilla* in North America (Kelly et al. 2002) and in the European robin on the Courish Spit (Tsvey 2008). In spring, a similar relationship was reported from several species of long-distance passerine migrants after crossing the Gulf of Mexico (Moore and Wang 1991). It cannot be ruled out that lower FDR recorded in hatching-year individuals as compared to adults in a number of species, e.g. in the Savi's warbler *Locustella luscinioides* in Portugal (Neto et al. 2008) and in bluethroats in Karelia (Panov and Chernetsov 2010) was also due to the higher competitive ability of experienced migrants.

High concentrations of songbird migrants at stopovers may increase both direct and interference competition (Salewski et al. 2007a) and decrease the energy efficiency of stopovers (Moore and Wang 1991). In one case (in the blackcap on the Courish Spit, Chernetsov and Titov 2001) the number of birds at stopover was positively, not negatively, related to FDR. The main food of blackcaps during autumn passage in this area is common elder *Sambucus nigra* which may be superabundant at times. Probably the highest concentrations of blackcaps at stopovers on Cape Rossitten were recorded when the common elder was very abundant, thus enabling a high FDR. It is also worth noting that densities of blackcaps in this area are never as high as e.g. those of European robins or goldcrests. Very high numbers of the latter species may indeed cause strong competitive interactions and inhibit their fuelling rate.

3.4.4 Food Availability

Apparently, most frequently FDR of stopover migrants should depend on food availability but this relationship is only infrequently formally shown. To obtain reliable estimates of food abundance for insectivorous or omnivorous songbirds, which are mostly long-distance migrants, is methodologically rather challenging (Grosch 1995; Eggers 2000; Salewski 1999; Chernetsov and Manukyan 1999a, b). As an example of such study one may make a reference to the research done in northern Spain (Grandío 1998). At a site with a high abundance of plum aphids sedge warblers increased their body mass by 0.96 g day^{-1} (SD = 0.23, n = 12), whereas at a poor site FDR was just 0.46 g day^{-1} (SD = 0.31, n = 22, Mann–Whitney test: $p < 0.001$). These values correspond to 9.3 and 4.6% of lean body mass. It is important that at both sites, trapping was performed simultaneously and within a short time interval, 5–11 August 1995, making the results comparable (Grandío 1998).

Sometimes foraging manoeuvres are studied as a proxy to food choice and abundance (Chen et al. 2011). It should be however noted that foraging manoeuvres in birds were suggested to be highly stereotyped (Khlebosolov 1993, 1996, 2005) and not very suitable for characterising highly variable stopover behaviour.

It has been shown that diet influences the composition of blood metabolites and thus probably the composition of fuel stores in long-distance migrants (Gannes 2001). Fruit-eating species, like blackcaps, garden warblers and lesser whitethroats, catabolised less protein and more lipids during their spring passage in Israel.

Apart from predictors that may be accounted for, there are other factors that influence FDR but elude analysis. These factors e.g. provided high FDR in European robins on the Courish Spit in the spring of 2001 and low FDR in the autumn of 1995, after other predictors had been taken into account (Tables 3.1, 3.2). These factors also result in high variance of FDR values typical of all the study sites (Dunn 2001, 2002; Tables 3.1, 3.2). An important factor for insectivorous birds is probably air temperature, as shown by the analysis performed by Schaub and Jenni (2001) on the basis of data from Rybachy on the Courish Spit. For pied flycatchers that forage on highly mobile aerial prey air temperature was an important predictor of fattening index, whereas FDR garden warblers in autumn, when they are largely frugivorous, was independent of weather variables (Table 6 in Schaub and Jenni 2001).

3.5 Low Initial FDR: Artefact or Real Phenomenon?

Many authors have reported that body mass of songbird migrants drops after their arrival to stopover and it is not until several days after arrival that they start to gain mass (Szulc-Olech 1965; Pettersson 1983; Hansson and Pettersson 1989; Loria and Moore 1990; Mädlow 1997; Wang and Moore 1997; Titov 1999a; Yosef and Wineman 2010).

3.5.1 Methodological Issues

It is usually assumed that at least two methodological issues seriously limit the value of these observations: first, the first capture does not always occur immediately after arrival; and second, capture and associated loss of foraging time and handling stress may significantly reduce foraging efficiency and FDR (Schwilch and Jenni 2001).

The former issue is less severe than it is often assumed. The first capture may indeed take place several days after arrival, but in areas with a pronounced wave-like pattern of passage (like the Baltic coast, where most of the aforementioned European studies were performed, or the Gulf of Mexico coast, where North American studies were made) most birds are captured soon after arrival (Titov and Chernetsov 1999b). The authors write that '[A]ssuming capture probability to be independent of time since arrival, only a minority of first captures have… arrived the night before' (Schwilch and Jenni 2001). This is correct, but it is the assumption that capture probability is independent of time since arrival that is unjustified, because the mobility of most migrants (which governs capture probability) sharply drops after one or two days at stopover (Chap. 6).

The problem of the possible effect of handling stress was analysed by Schwilch and Jenni (2001) in much detail. These authors measured the plasma levels of triglycerides and β-hydroxybutyrate and showed that fattening rate did not differ between Eurasian reed warblers that had just arrived at the stopover site (tape-lured into the area) and those that had been there already during several days. The FDR of birds captured twice in one day was not lower than of those trapped only once. The authors claimed that since at their study area (Wauwiler Moos in Switzerland) mist-nets were checked every 20 min, and not every hour, which is the routine at most mist-netting sites (Bairlein 1995, 1998), mass change values, though negative, but not significantly different from zero, the trapping effect could be considered absent. It was different from two other Swiss sites (Portalban and Bolle di Magadino) where recapture data suggested mass loss on the day of capture (Schwilch and Jenni 2001).

I believe that the authors' claims are too far-fetched. The mean mass change on the day of capture in Wauwiler Moos was negative and, most importantly, significantly different from the positive value of mass change on the subsequent days (Fig. 3 in Schwilch and Jenni 2001). A similar pattern was observed at other trapping sites (Fig. 4 in Schwilch and Jenni 2001). Besides, the claim that the tape-lured Eurasian reed warblers had just arrived, whereas the individuals trapped without song playback had arrived several days before capture, is not undeniable (see above). Contrary to the authors' viewpoint, their data does not refute the opinion that migrants lose body mass on the first day upon arrival at stopover. In Louisiana, after crossing the Gulf of Mexico in spring, the probability of losing body mass in red-eyed vireos was not related to the number of recaptures (Loria and Moore 1990), i.e. handling stress is not the only reason for initial mass loss.

Recaptures and radio-tracking data suggest that mobility of many passerine migrants on the day of arrival to stopover and partly on the second day is significantly higher than on subsequent days (Chap. 6). It seems probable that during the first 1–2 days after arrival migrants select the optimal habitat and occupy temporary home ranges, i.e. perform search/settling activities, and only after they are settled, they start to refuel at the maximum possible rate. It happens even when no major barrier crossing is involved, when many passerines reduce their digestive organs during long-distance flights and need to build them up before they are able to forage at the maximum rate (Hume and Biebach 1996; Biebach 1998; Bauchinger and Biebach 1998; Karasov and Pinshow 1998). Low and sometimes even negative FDR on the first day of stopover in passerines is not an artefact caused by handling stress, but a rather widespread event.

3.5.2 Physiological and Ecological Constraints

Low initial FDR may be due to physiological constraints, especially after endurance flights when crossing ecological barriers (Karasov and Pinshow 1998; Biebach 1998; Bauchinger and Biebach 2001, 2005; Bauchinger et al. 2005), or due to difficulties that a migrant faces after completing flight and arriving at a novel area (see Chap. 5). The latter situation, i.e. ecological difficulties settled by behavioural adaptations, is probably the main reason for low FDR on the first day(s) after arrival when no barrier crossing is involved.

All data on digestive tract reduction that inhibits efficient foraging immediately after completing migratory flights, in songbirds (see the aforementioned references) and in waders (Piersma 1998; Piersma and Gill 1998; Piersma et al. 1999; Battley et al. 2000, 2001), refer to very long endurance flights. No data available suggests that similar changes may occur during migration with continuous stopover possibility, i.e. without very long flights. It seems that in such situations no significant reduction of the digestive tract occurs that might cause physiological difficulties for foraging at the maximum rate possible.

As body mass decline within 1–2 days upon arrival at stopover in songbirds is usually explained not by their physiology but by ecology (search/settling difficulties), in some optimal habitats this decline may not happen (Bairlein 1987; Moore and Kerlinger 1987; Carpenter et al. 1993). However, analysis of the literature suggests that body mass drop soon after arrival occurs more often than not.

A significant consequence of this is that FDR is generally not stable during the stopover period. At the beginning of a stopover FDR is small or even negative. Later on, if a migrant remains in the area, it increases. The optimal migration theory assumes that when the migrant reaches a certain threshold of fuel stores (optimal departure fuel load, with optimality defined by various parameters, and, no less importantly, by the researcher's many assumptions), it takes off, thus completing the stopover. This model however assumes that departure decision is made on the basis of energetic considerations only. In the wild, however, other factors are in play as well, in particular the weather (Liechti 1995, 2006; Liechti and Bruderer 1998; Åkesson and Hedenström 2000; Schaub et al. 2004; Tsvey et al. 2007). It is not known how large or small FDR is in a migrant that has reached the threshold fuel load but is delayed by the adverse weather. In some cases under such circumstances body mass may decrease again, which was found in whitethroats in Sweden (Fransson 1998) and in Eurasian reed warblers in Israel (Merom et al. 2000). The data on FDR of sedge warblers in England also supports the existence of such effect: both the mass increase rate during the day (coefficient *a*) and the net FDR (coefficient *b*) declined towards the day of departure (Bayly 2007). It cannot be ruled out that FDR declines in the last days preceding departure not only because of the adverse weather (which prevents departure), but also due to the elevated existence costs with high fuel stores (Klaassen and Lindström 1996).The latter authors assume that large fat stores have high metabolic costs of their maintenance, even though it should be kept in mind that adipose tissue is metabolically rather inert, therefore direct metabolic costs of its maintenance are not very high (Schmidt-Nielsen 1997). Moreover, fat individuals have higher costs of locomotion (especially of flight) and may have an inferior ability to escape predators (but see below, Sect. 4.4).

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