Chapter 8
Migratory Flights and Stopovers: Organisation of Migration

Abstract In this chapter I summarise the contents of this monograph and propose the model that four main groups of factors influence the decision to take off: current fuel stores, fuel deposition rate at a given stopover site, weather factors (mainly wind assistance) and geographic position relative to the optimal rate of migration. I also discuss the principles of organisation of migration in songbirds and different selection pressures that may govern migration from the breeding to the non-breeding area and back. This chapter also contains the main conclusions, and after them I outline the future research directions that may bring further progress to the field. The alternation of flights and stopovers is apparently organised in some manner. The aim of our study is to identify the principles that govern this organisation of migration. Flights are dependent on stopovers in an apparent way: during flights, the energy stored during the stopovers is used. Therefore it is necessary to obtain estimates of the energy deposition rate at stopovers and of the rate of using energy during flights.

8.1 The Importance of Fuel Deposition Rate

As shown in Chap. 3, FDR in the wild is usually rather low, and the maximum known values follow the equation $\mathrm{FDR}_{\max} = 2.17\ \mathrm{mass}^{-0.34}$, where mass is body mass in kilograms (Lindström 2003). This means that a Eurasian reed warbler with the lean body mass of ca. 10.0 g under optimal conditions can increase its body mass by 1.04 g per day. Assuming the energy density of fuel stores of 21.6 kJ g^{-1} (Klaassen et al. 2000) and flight power of 5.80 kJ h^{-1} (Sect. 7.7), one day of fuelling at the maximum possible rate provides a Eurasian reed warbler with energy sufficient for flying during 3.9 h. The duration of an average nocturnal migratory flight during spring passage in this species is 4.1 h (Bolshakov et al. 2003a), i.e. the energy gained during one day of feeding ad libitum is nearly sufficient for

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one night of flight. For comparison, a European robin can gain a maximum of 29.2 kJ of energy in one day, with allows it to fly during 3.7 h, assuming the flight cost of 7.1 BMR and BMR = 26.45 kJ day^{-1}, which is the mean of the four published estimates: 26.0 (Gavrilov 1980); 29.1 (Gavrilov 1985); 24.3 and 26.4 kJ day^{-1} (Gavrilov 1981).

These calculations predict the maximum possible fuel deposition rate. The FDR that is reached in the wild is usually much lower due to food shortage, competition, predation risk etc. (Chap. 3). Besides, in the first 1–2 days upon arrival at stopover FDR may be very low, or even negative (Szulc-Olech 1965; Pettersson 1983; Hansson and Pettersson 1989; Mädlow 1997; Titov 1999; Sect. 3.5). Obviously, such a hitch at the beginning makes the mean FDR across the overall time of stopover much lower. Therefore, in the real world migrants need much longer than a single foraging day to gain energy necessary to fly during 3.7–3.9 h.

It should be also kept in mind that the FDR values observed in the wild always show a large dispersion, and the significant predictors (e.g. initial fuel load) often leave a great deal of variation unexplained (Chernetsov and Titov 2001; Chernetsov et al. 2007). As an example, we can look into FDR values of Eurasian reed warblers, sedge warblers and garden warblers at several European and North African sites during autumn migration (Schaub and Jenni 2000). In the Eurasian reed warbler the proportion of explained variance in FDR in the best generalised linear model varied between 21.2 – 64.9% (13 sites); in the sedge warbler, between 26.0 and 38.4% (seven sites, the value for Mettnau, SW Germany [97.4%] is omitted because it is based on the analysis of only 10 recaptures); in the garden warbler, between 0.1 and 69.2% (12 sites). The highest proportion of explained variance among the sites where >100 recaptures were included was 42.5% (FDR of Eurasian reed warblers in Mettnau). The predictors were stopover duration, initial body mass, the progress of season and moult status. Thus, about one-half of variance in FDR usually remains unexplained.

8.2 Factors that Govern Departure Decisions

The main currency that shapes the organisation of migration is the energy necessary for flight (and safety, i.e. the probability to survive; see Chap. 4). As shown by both field and experimental data, fat individuals are more prone to take off than lean ones (Wang and Moore 1993; Jenni and Schaub 2003; Fusani et al. 2009). However, it is not possible to construct a realistic and generally a heuristically useful model of the migratory strategy of passerines on the basis of energetic considerations alone. As shown in Chap. 4, the attempts made in the framework of the optimal migration theory cannot be called successful. They did not result in the models that would fit the data well enough, because apart from the energetic (i.e. endogenous) factor, the behaviour of the migrants is strongly modified by the environment.

Apart from the variation in fuel deposition rate during the stopover period, departure decisions are strongly influenced by the weather, mainly by wind speed and direction (Schaub et al. 2004; Tsvey et al. 2007; Arizaga et al. 2011; Schmaljohann et al. 2011; Schmaljohann and Naef-Daenzer 2011). It should be mentioned that Victor Bulyuk and Arseny Tsvey (*in litt.* 2011) analysed weather conditions on the nights of departures of European robins that stopped over on the Courish Spit for more than one day and were captured in mist-nets at take-off. The weather on the nights of departure of such birds was not significantly different from the that in the preceding nights. However, it should be kept in mind that some of the recorded departures could be for exploratory flights (Schmaljohann et al. 2011; Mills et al. 2011), or the birds might abort their departures. This may or may not be recorded when radio-tracking the birds, but captures in elevated mist-nets do not allow to distinguish between the 'true' (or 'successful') migratory departures and the exploratory or aborted flights.

What happens after an aborted flight? In practice, the stopover continues. Does the migrant continue to gain fuel if the environmental conditions permit it? Such situations may occur not infrequently in September and October in northern and central Europe, when the weather conditions unfavourable for flight (opposing westerly and south-westerly winds) are favourable for refuelling (relatively high air temperature; Chernetsov 2002). Isolated cases of captures of very heavy birds not in front of a barrier, i.e. of European robins with the body mass exceeding 20 g (i.e. fuel load ca. 50%), sedge warblers weighing 18–19 g (fuel load ca. 80–90%), a great reed warbler weighing 45.5 g (Koleček 2006) seem to support this viewpoint. It should be however kept in mind that such captures of very fat individuals are very rare. On the other hand, as we have already mentioned more than once, mist-netting probability of a songbird depends on its mobility, and the mobility of the individuals with high fuel loads may be very low. Because of that, heavy migrants may be strongly underrepresented in captures and be more common in the wild than usually assumed (Kosarev and Kobylkov 2010).

The weather, including wind, may influence not only migratory departures but also the decision to cease flight. When crossing the Sahara, passerine nocturnal migrants continue their flights after daybreak if they enjoy following winds and land in the desert if the wind is opposing (Schmaljohann et al. 2007a). Emergency landing at night is well known when flight conditions quickly deteriorate. For instance, mass emergency landing of migrating thrushes, mainly song thrushes, was recorded in Lithuania on 23 October 1990 when the weather favourable for migratory flight was sharply replaced by low clouds and fog (Bolshakov et al. 2002).

The most realistic qualitative model of behaviour of migrants at stopover may be presented in the following way. Any migrant is influenced by at least four groups of factors that are to some extent independent on each other and thus may be represented as orthogonal axes in the four-dimensional hyperspace: (1) current energy status; (2) habitat quality that makes it possible to reach a certain FDR; (3) weather conditions, first of all wind assistance; and (4) position on the migratory route with respect to the individual schedule of migration. Most prone to continue migration, i.e. to depart, are fat birds at a poor site under weather conditions favourable for flight that are delayed on the migratory route (i.e. because of unfavourable weather in the preceding days). The position of a migrant along any of these axes influences its readiness to migrate: under favourable weather conditions both fat birds depart (that would have departed also in poorer weather) and their leaner conspecifics that in worse weather would have remained at stopover. There is evidence that the optimal schedule of migration may be individually adjusted, as shown by the data at the onset of spring migration of bar-tailed godwits from New Zealand (Battley 2006; Conklin et al. 2010) and from Portugal (Lourenço et al. 2011). If migration is much delayed (like in late May—early June 1974 on the southern coast of the Gulf of Finland in the European robin; Bolshakov and Rezvyi 1998), nearly all individuals depart for migratory flights, even those whose fuel stores are low. This is probably what Tatiana Blyumental and Victor Dolnik meant when they wrote about 'carrying along of the lean individuals by the fat ones' when explaining how the waves of migration were formed (Blyumental et al. 1967; Dolnik and Blyumental 1967; Dolnik 1975). This 'carrying along' was postulated when discussing the migration of fringillid finches, i.e. short- and medium-distance diurnal migrants (Dolnik 1975); its existence in solitary nocturnal migrants seems dubious. After the periods of strong opposing winds which are very unfavourable for migration on the Courish Spit significantly more European robins take off under moderate opposing winds, i.e. with negative wind assistance (Bulyuk and Tsvey *in litt.* 2011). Recent radar studies have shown that songbirds perform migratory flights with negative wind assistance more often than hitherto assumed (Karlsson et al. 2011).

The influence of stopover habitat quality on the departure decision has been shown experimentally. European robins and pied flycatchers in migratory disposition stopped to show migratory restlessness (Zugunruhe) if after a period of fasting (which imitated migratory flight) they were fed ad libitum. Zugunruhe resumed when food access was again restricted, imitating poor stopover site (Merkel 1938, 1958; Biebach 1985; Gwinner et al. 1988). In the field experiment Eurasian reed warblers tape-lured into a suboptimal habitat (sand dunes on the Courish Spit) departed from the stopover site by nocturnal migratory flights (Ktitorov et al. 2010). All individuals, even the lean ones, left the area by nocturnal flights on the first night after arrival ($n = 10$).

Our model assumes that the values of each factor which releases flight are not fixed, but vary within certain limits which are defined by other factors. This makes it possible to explain why birds captured at migratory take-off show a broad variation of body mass and fuel load values (Sect. 7.2). This range of variation does not support the idea of the threshold fuel load releasing flights. The weather conditions under which migrants depart (Bulyuk and Tsvey 2006; Bolshakov et al. 2007; Tsvey et al. 2007; Bulyuk and Mukhin 2010) and fly (Richardson 1978, 1990; Bolshakov 1981; Karlsson et al. 2011) also vary broadly. Some individuals start and perform migratory flights under the most inclement weather conditions, which permitted Victor Dolnik to claim that "with respect to birds it is a mistake to use the words 'flying' or 'non-flying' weather: migratory birds are practically all-weather aircrafts" (Dolnik 1975, p. 41). Certainly this does not mean that the weather conditions do not influence bird migration. However, whatever factor we analyse in isolation, the migratory flights may be performed (and start) at so broad a range of its values that a migratory flight may be initiated by any individual in any condition. Only the analysis of the combination of the aforementioned factors may help identify the patterns.

It should be mentioned that this model is actually just an application of the well-known limiting factor rule (Begon et al. 2006) to movement ecology of birds: of the four suggested groups of factors of the greatest importance for the departure decisions is the one which is the closest to the critical (i.e. prohibiting) value.

It should be also kept in mind that the independence of the four groups of factors (and, as a consequence, the orthogonality of the representing axes) is rather conventional. The current energy condition of the migrant is only independent of the habitat quality at the stopover site immediately after arrival (and even habitat selection during arrival may be and most probably is condition-dependent). During stopover the latter factor greatly influences the former one. Current weather (its suitability for migratory flights) is often correlated with the weather during the preceding days, which may influence the fuel deposition rate (especially in early arriving individuals in spring) and the position of the bird with respect to its migratory schedule. However, the assertion that 'every factor depends on all the others' may be formally correct but is not very enlightening. Therefore I suggest that there is a point in isolating groups of relatively independent factors but the conditional character of their independence should be retained.

8.3 Series of Migratory Flights and Waves of Passage

Small passerines that resume migration after a successful prolonged stopover usually appear to make several nocturnal flights in succession. A series of migratory flights starts when migrants accumulate sufficient fuel stores; its onset seems to be mainly governed by energy and the spatiotemporal migratory programme (Dolnik and Blyumental 1967; Dolnik 1968, 1975; Berthold 1996, 2001; Jenni and Schaub 2003). It seems that migrants that resume migration after prolonged stopovers may depart under a broad range of weather conditions (Bulyuk and Tsvey 2006; Tsvey et al. 2007; Bulyuk and Mukhin 2010). If the weather is favourable for migratory flights, migration may continue beyond the first night. A relatively small energy cost of flying in good weather (low air turbulence, significant wind assistance) further favours flying during several nights. Between these nocturnal flights migrants make one-day stopovers, i.e. they are transients at the respective stopover sites. This tactics of migration seems to be typical of songbird long-distance migrants both in spring (Bolshakov et al. 2003a, b; Tøttrup et al. 2012) and in autumn, as shown by the analysis of ring recoveries (Fransson 1995; Hall-Karlsson and Fransson 2008).

The study of the temporal schedule of nocturnal departures of European robins showed that their readiness to take off after one-day stopovers and partly departure time were mainly defined by the weather in the preceding night, i.e. during the previous flight (Bulyuk and Tsvey 2006). European robins can continue the series of migratory flights if they have previously migrated with following winds and have not depleted their fuel stores. Conversely, if the flight occurred under unfavourable winds and resulted in large expenditure of energy, the series of flights is terminated (Dolnik and Blyumental 1967; Dolnik 1975). It cannot also be ruled out that progress towards the goal of migration may also influence the decision to continue flights. It is generally assumed that first-time migrants have no information about the goal of their migration (Gwinner and Wiltschko 1978; Berthold 1990, 1996). However, evidence is accumulating that first-autumn migrants can control their position on the migratory route on the basis of external references, in particular of the geomagnetic field parameters (Beck and Wiltschko 1988; Wiltschko and Wiltschko 1992; Fransson et al. 2001; Kullberg et al. 2007; Chernetsov et al. 2008; Henshaw et al. 2008, 2009).

Anyway, wind assistance is apparently one of the most important extrinsic factors that govern the decision to continue migration or terminate it. It should be emphasized that before migrants take off, they seem to have no ‘miraculous’ method to know the high-altitude wind. The only way to know the wind at the normal flight altitudes is to take off and to test it, as suggested by exploratory flights of northern wheatears on Helgoland (Schmaljohann et al. 2011) and by aborted departures of European robins on the Courish Spit. Changes in wind conditions may synchronise the cycles of migratory activity of individual migrants (Dolnik and Blyumental 1967; Dolnik 1975; Schaub et al. 2004). As a result, the dynamics of passage often (but not always) has a pronounced wave-like pattern, when peaks of passage are alternated with much quieter nights (Bolshakov 1981; Erni et al. 2002). As some migrants may be at different stages of the series of migratory flights (some may be starting, some continuing, and some finishing them) individual migrants that arrive at a stopover site on the same night, may show broad variation in fuel stores and stopover duration (Tsvey et al. 2007).

A series of migratory flights comes to an end when fuel stores of migrants are depleted and/or when the weather deteriorates. Using such migratory tactics during autumn migration may be adaptive to the unpredictable and often unstable weather. In autumn in northern and north-eastern Europe such behaviour allows the birds to migrate towards the south-west in spite of dominating opposing winds and allow them to use improvements in the weather conditions in the optimal way. The same tactics is optimal during spring migration in Europe, when warm weather which significantly improves feeding conditions for insectivorous migrants is usually caused by intrusions of warm air from the Mediterranean, which also provide favourable conditions for northbound flights (Chernetsov 2002; Bolshakov et al. 2003a). In other regions and seasons, when opposing winds are less frequent, the ability to fine-tune migratory behaviour to the weather conditions might be less crucial.

The results of such tactics of migration are apparent from the analysis of daily variation in trapping numbers. New individuals arrive at stopover after nights with any wind direction. However, the numbers of European robins peak after the nights with following winds (Bulyuk and Tsvey *in litt*. 2011). On some nights the numbers of arriving migrants also increased in the nights with weak or moderate opposing winds, when they followed the nights with strong opposing winds (Bolshakov and Rezvyi 1998; Erni et al. 2002). Therefore, the weather conditions may synchronise the series of migratory flights performed by different individuals and help formation of the waves of passage recorded by visual observations or in trapping projects (Blyumental et al. 1967; Dolnik 1975).

Songbird migrants take off under different weather conditions, but quickly abort their flights when the wind is unfavourable (Schmaljohann et al. 2011). If the wind is favourable (in spring) or at least less unfavourable than in the preceding days (in autumn), a large number of birds continue flight, so that a migratory wave is formed. If the favourable weather persists, the fuel stores of migrants are used up rather slowly, so that migratory flights can be performed during several nights is succession. In such case a strong wave of passage is observed, like it was shown for fieldfares during spring migration (Bolshakov 1992). In the areas where the weather conditions during the migratory season are very stable (e.g. in the Central Asian deserts), the flow of migrants may be very uniform during several weeks, without any waves.

8.4 Spring Versus Autumn Migration

Spring and autumn migration (to be more exact, migration to and from the breeding quarters) mainly differ in that in spring most adult passerines return to their previous breeding area (i.e. show breeding site fidelity), and many yearlings head for the area that they have imprinted as the future breeding site during postfledging movements in the previous year (Sokolov 1997; Newton 2008; Grinkevich et al. 2009). Without discussing the mean distance of natal dispersal in passerines (e.g. Paradis et al. 1998), we can safely claim that a very significant proportion of first-time breeders returns to the area whose linear size is by 2–3 orders of magnitude smaller than their migratory distance. This has been repeatedly shown by ringing recoveries. It means that in spring, all or most migrants have a certain migratory goal, whereas during autumn migration, only adult experienced individuals may have a goal. First-autumn migrants fly towards the areas they have never visited before. The currently accepted clock-and-compass concept assumes that juvenile migrants have no inherited knowledge of their migratory destination except of the (necessarily general) inherited programme but the recent data suggests that this view may be challenged (see Sect. 1.2).

It cannot be ruled out that the existence of a certain narrow migratory target in spring and its absence in many first-time migrants in autumn may influence their migratory behaviour. It has been shown that at least some individuals of long-distance songbird migrants arrive in spring at their breeding sites by nocturnal flights (Bulyuk 2006) and do not perform any slow search in the daytime as it has been believed for a long time (Heinroth and Heinroth 1941). These data indicate a very precise, pinpoint navigation of nocturnal migrants during their flights, with an accuracy of ca. 1 km. It is most likely that these birds took off from different last stopover areas and started their flights at different time after sunset. The distance to the goal of migration may be an important factor that influences the timing of migratory departure in spring (Bolshakov and Bulyuk 1999; Bolshakov et al. 2007).

Apart from these factors that are universal, variation caused by regional weather features, for instance, the direction of the prevailing winds may exist. In central and northern Europe in spring warm periods, when the activity of invertebrates increases and thus food availability for insectivorous migrants improves (Chernetsov and Manukyan 1999, 2000), are usually caused by the intrusions of warm air from the Mediterranean region. These southerly or south-westerly winds provide good wind assistance for most songbirds migrating in spring in this region. Therefore, in spring the same synoptic weather situations are favourable for both migratory flights and stopovers. It allows the migrants to perform several flights in succession and to move towards their migratory target quickly (Bolshakov et al. 2003a, b). This behaviour is very adaptive because in spring many avian migrants, especially males, benefit from early arrival at their breeding grounds, and the bonus for early arrival may be very significant at least for some individuals (Kokko 1999; Forstmeier 2002).

In autumn, in the same region warm south-westerly winds influence favourably food availability for insectivors, but are opposing to and thus unfavourable for migratory flights. As a result, wind selectivity of passerine migrants may vary between different years: is some years migrants are less selective than in others, probably because of the rarer occurrence of favourable winds (Tsvey et al. 2007). This situation is a special case of the more general rule described in Sect. 8.2.

Apparently, in other regions of the Earth weather (mainly wind) conditions prevailing in the respective seasons may influence bird migration in a different manner. Europe and eastern North America are relatively well studied in this respect, whereas the patterns that occur in other regions are very poorly known and cry for research into the regional aspects of avian migration (e.g. studies in Central Asia: Dolnik 1990; Bolshakov 2002, 2003; Raess 2008; in temperate East Asia: Wang et al. 2006; Yamaguchi et al. 2008, 2012). These studies can also shed light on the basic patterns of avian migration.

8.5 Annual Movements of a Typical Long-Distance Passerine Nocturnal Migrant

Let us imagine a typical long-distance avian migrant, for example a Eurasian reed warbler, breeding in Eastern Europe. Juvenile Eurasian reed warblers start their nocturnal postfledging movements early, when 35–40 days old (Mukhin et al. 2005).

The function of these nocturnal flights is still unclear. They might be necessary to form the navigational target to which they will try to return the next spring, or to develop flying and orientation abilities (Mukhin et al. 2005). However, the birds do not start to migrate, i.e. to consequently move in the migratory direction until they are 50–55 days old (Mukhin 2004). By the age of 60 days all juveniles will have left their natal area and started autumn migration (Chernetsov and Mukhin 2001). Therefore, most Eurasian reed warblers start autumn migration in mid—late August. Most adults start their autumn migration even earlier, in late July, and overlap it with body moult, even though this overlap is more typical of passerines breeding further north, in the boreal forest and tundra (Panov 2011).

It has been shown in several long-distance passerine migrants (the most considerable material was obtained for the Eurasian reed warbler) that adults start their first nocturnal flight during autumn migration with relatively large fuel stores, on average 17.6% of their lean body mass (SD = 5.6, n = 6; Bulyuk 2010). The mean body mass of adult Eurasian reed warblers that took off for their first migratory flight from the breeding area was practically indistinguishable from the values typical of adult transients (Bulyuk 2010). It strongly suggests that adults start migration in the developed migratory disposition, and the first nocturnal flight may be rather long-range. The preliminary radio-tracking data suggests that the situation in first-autumn Eurasian reed warblers may be similar (Kosarev and Kobylkov 2010). However, in many species and populations of long-distance migrants migratory speed increases with the progress of migration (Hedenström and Pettersson 1987; Ellegren 1990, 1993), therefore, early during autumn migration flights may be shorter, and stopovers longer (Panov 2012).

Eurasian reed warblers from the Eastern Baltic migrate through the Iberian Peninsula (Chernetsov 1999), the distance to which is ca. 2,000 km; other long-distance migrants cover some 1,500 km to the Mediterranean coast. The mean speed of migration (i.e. movement along the migratory route with stopover time considered) in Eurasian reed warblers ringed in central Sweden was on average 39 km day^{-1} (Bensch and Nielsen 1999), i.e. the birds should need some 50 days to cover 2,000 km. It is however conceivable that the speed was underestimated in this study, because some individuals had been ringed during postfledging movements before their actual migratory departure. In other long-distance songbird migrants the estimates of migratory speed are higher: in Swedish sedge warblers it was on average 55 km day^{-1} (Bensch and Nielsen 1999), in *Sylvia* warblers varied between 43 and 93 km day^{-1} depending on species and the area of origin (Fransson 1995). Assuming such estimates, the Mediterranean may be reached more quickly, in 25–40 days. Red-backed shrikes supplied with geolocators travelled from the southern Baltic coast to SE Europe with the average speed of 101 km day^{-1} and reached that area in only 9 days (SD = 5.1; n = 9; Tøttrup et al. 2012).

In late September our Baltic Eurasian reed warbler reaches the northern edge of the extensive ecological barrier which is formed by the Mediterranean and the Sahara, and starts to fuel up. Until now, migration occurred without accumulating large fuel loads that would significantly increase the energy cost of flying

(Sect. 3.5), but now the migrant has to accumulate significant fuel stores (at least 50% and up to 100% of its lean body mass) that make the flight significantly more expensive, in line with the predictions of the aerodynamic theory.

The current data obtained by large-scale radar studies of passerine migration in the Sahara clearly show that the main strategy of crossing the desert is flight during the day and rest in the desert during the night (Schmaljohann et al. 2007a, b). The concept of non-stop flight across the desert suggested by Reginald E. Moreau half a century ago suggesting that migrants fly non-stop during several days (Moreau 1961) has raised doubts for quite some time (Bairlein 1985, 1988; Biebach et al. 1986), and now can be considered refuted (Schmaljohann et al. 2007a, b; Salewski et al. 2010). However, from the energetic viewpoint it makes the situation for the migrants more, not less, grave: during the diurnal rest the distance to the goal (relatively suitable stopovers areas on the northern edge of the Sahel) is not reduced, and the energy continues to be consumed (assumed at ca. 0.5% of body mass per hour; Meijer et al. 1994; Salewski et al. 2010).

After crossing the Sahara in tropical Africa different passerine migrants utilise very different spatial strategies. Some species, like the pied flycatcher (Salewski et al. 2002) or bluethroat (Markovets and Yosef 2005) occupy a territory where they spend the whole winter and where they recur every year. Other long-distance migrants, e.g. the willow warbler or garden warbler, move broadly within Africa, so that their movements may be called intra-African migration (Jones 1995; Salewski et al. 2002; Ottosson et al. 2005). Red-backed shrikes remain for 1–2 months in the Sahel/savannah zone of southern Sudan before they proceed to their final winter quarters in Botswana/Angola (Tøttrup et al. 2012). I suggest that their stay in Sudan, which is also typical of several other Palaearctic migrants, namely the marsh warbler, great reed warbler and whitethroat (Yohannes et al. 2009b), should be called the first winter quarter rather than stopover (cf. Introduction), and their movements between the first and the final winter quarters is intra-African migration. Little is known about the physiological basis of these movements (Terrill 1990).

The onset of spring migration is very poorly studied. It is one of the least known periods of the annual cycle in long-distance passerine migrants; recently, when radio-tracking has greatly advanced our knowledge of the postfledging period before the onset of autumn migration (Vega Rivera et al. 1998, 2003; Mukhin 2004; Mukhin et al. 2005), it probably became the least studied period.

It is believed that the onset of spring migration is under endogenous control (Berthold 1996), but recently some data has became available suggesting that this trait, too, may be modified by the environment, in particular, by precipitation in the wintering area (Sokolov and Kosarev 2003). In any case, migratory speed in spring is much higher than in autumn, as shown by the analysis of ring recoveries (Fransson 1995; Hall-Karlsson and Fransson 2008; Yohannes et al. 2009a) and by geolocator tracking data (Stutchbury et al. 2009; Heckscher et al. 2011; Tøttrup et al. 2012). It is usually assumed that the main reason for that is the necessity to arrive first to the breeding areas, because first arrivals, especially males, can occupy optimal breeding territories (Kokko 1999). As mentioned earlier, in spring

European long-distance migrants enjoy the weather situations favourable for migratory flights simultaneously with the weather situations favourable for foraging and fuelling. In the very recent years, information on the departure time and travel speed of songbirds from their winter quarters in South America (Stutchbury et al. 2009) and Africa (Tøttrup et al. 2012). Spring migration may be remarkably rapid: two purple martins travelled from Brazil to Pennsylvania in 13 and 27 days; wood thrushes returned to Pennsylvania from Honduras or Nicaragua in 13–29 days (n = 6; Stutchbury et al. 2009); similarily, veeries travelled from South America to Delaware in 17–33 days (n = 5; Heckscher et al. 2011). More data will most probably become available very soon.

In the recent years, the season of spring migratory arrival in most passerines, long-distance migrants included, has shifted towards earlier dates (Moritz 1993; Mason 1995; Sokolov et al. 1998; Sokolov and Payevsky 1998; Sokolov 2000, 2006; Crick and Sparks 2006; Gordo 2007; Møller et al. 2010). In western Europe, where winters have become much milder and spring phenology has advanced a lot, the advancement of arrival dates of long-distance migrants is insufficient, resulting in the mismatch between time of reproduction and the peak of resources: even though birds breed earlier in calendar dates, phenologically they breed later than in earlier years (Both and Visser 2001; Both et al. 2005, 2010). Many passerines, e.g. pied flycatchers in the Netherlands, breed now phenologically too late, in the suboptimal season. However, in other regions, where spring phenology has not (yet?) advanced so much as it did in western Europe (i.e. in the Urals or in Siberia), no such mismatch is currently observed (Sokolov and Gordienko 2008; Ananin and Sokolov 2009).

8.6 Conclusions

1. Passerine migrants usually stop over for 1–15 days. Sometimes, especially before and just after crossing large ecological barriers (large water bodies, deserts) stopovers may be longer and reach 20–25 days. Significant proportions of migrants stop over for one day only and continue migration on the first night after arrival. When studying stopover behaviour by stochastic capture-mark-recapture models, it is most useful to estimate the proportion of ‘transients’ (migrants that make one-day stopovers) and the mean stopover duration of non-transients. However, it should be kept in mind that capture-mark-recapture models tend to overestimate the number of transients, whereas radio-tagging results in more realistic estimates.
2. The mean fuel deposition rate (FDR) during migratory stopovers varies between zero and even negative values to 0.5% of lean body mass per day, but theoretically under ideal conditions may be as high as 10% per day. FDR does not remain constant during the stopover: it is low or even negative during the first 1–2 days upon arrival, then increases and may decrease again in the last

days of a prolonged stopover, especially if migratory departure is delayed by adverse weather. The mean FDR is often inversely related to the initial body mass. During the autumn migratory season FDR may increase with the progress of the season, even when food abundance and availability decline. FDR broadly varies on the individual basis; a large proportion of its variation is not explained by the extrinsic factors.

3. The relationships between the main energetic parameters of migratory stopovers (fuel deposition rate, stopover duration and departure fuel load) are usually described in the framework of the optimal migration theory. This theory is the accepted paradigm in the bird migration research, and the study of movement ecology and behaviour and of the evolution of migration is usually performed in this framework. Analysis of the original and literature data calls the correctness of this framework in question. The idea of the U-shaped relationship between flight speed and flight power, which is fundamental for the optimal migration theory, is not supported by the empirical data. In long-distance songbird migrants, i.e. birds adapted to endurance flapping flight, energy cost of flight is independent of its speed in a broad range of flight velocities. Up to the fuel loads of 25–30%, the transport of extra load (fuel) is nearly free, and the potential flight range is directly proportional to fuel load. The existing concept is a result of application of the fixed-wing flight theory to the avian flight which is non-stationary.

   A serious weakness of the optimal migration theory is that its predictions are difficult to test. By varying the initial assumptions, it is possible to change model predictions in such a way that they will agree to practically any field data. However, the idea of finding qualitative and quantitative relationships between the energetic parameters of migratory stopovers is a very useful one; it has greatly advanced avian migration research.
4. The correct selection of the optimal habitat during migratory stopovers plays a great (often decisive) role for safe and successful migration. Nocturnal migrants usually solve this problem by using visual cues when landing after migratory flights. The number of individuals that fail to recognize correctly their habitat is usually small; it usually happens under the conditions of poor visibility (rain, fog). Wetland passerines use for habitat recognition not only visual but also acoustic stimuli. They respond not only to the conspecific vocalisations but also to heterospecific song typical of the certain habitat (i.e. to the acoustic habitat markers). The response to song is either inherited or is developed early in life. Migrating passerines often have to utilise habitats significantly different from those they prefer during breeding. Apart from the immediate habitats, the broader landscape context is also an important factor which shapes the quality of a stopover site for migrants.
5. An extreme case of selection of an optimal habitat patch in the inhospitable matrix is stopping over on islands and in oases. The hypothesis that oases are ecological traps for stopover migrants that cannot refuel there because of their small carrying capacity and competition is not supported by the field data. Even

on small islands and in small oases the mean FDR is usually not much lower than in continuous habitat.

6. Daytime movements of nocturnal migrants do not refer to migratory activity and are habitat- and foraging-related. Usually they occur towards optimal habitats and are not generally directed towards the goal of migration. The exception is to so-called morning flights that at least in some cases are performed to compensate for wind drift during the preceding long-distance migratory flight, and migratory movements of migrants with the mixed rhythm of diel activity (*Turdus* thrushes, goldcrests, bramblings *Fringilla montifringilla* etc.).

   Spatial behaviour of passerines at migratory stopovers is very variable. Some species, e.g. the European robin, after ceasing migratory flight move across hundreds of metres and either resume flight on the first or second night upon arrival or occupy a restricted home range (some species defend it) and remain there until the end of stopover. Other species, e.g. pied flycatchers in spring, move broadly looking for locally abundant food throughout the stopover period. It is not inconceivable that the same species of migrants may employ different spatial strategies depending on the ecological conditions at stopover. The main factor that governs spatial stopover behaviour is the spatio-temporal distribution of the preferred food. If the food is relatively uniformly distributed in space and predictable in time, the migrants tend to occupy (and sometimes to defend) small home ranges. Species that utilise patchily distributed and unpredictable food sources make broad movements.
7. The current concept of the temporal schedule of nocturnal migratory flights is not accurate. The synchronised departures at the beginning of the night are only typical of migration during short nights (mainly in spring at temperate and high latitudes). When nights are long, many take-offs occur long after the end of the evening twilight. Fuel loads of departing migrants vary broadly and often are not significantly higher than the mean fuel loads of migrants at stopover. Some birds initiate nocturnal flights with rather small fuel loads. They may be making short flights in the migratory direction, and may be performing landscape-scale nocturnal flights aimed at habitat optimisation in reverse or any other direction.
8. The rate of energy expenditure in migratory flight in long-distance passerine migrants, adapted to endurance flights, is 6–7 times higher than their basal metabolic rate (BMR). This is much lower than the value of 10–12 BMR hitherto assumed (Dolnik 1995; Berthold 1996). The data from both free-flying birds and wind tunnel experiments provide evidence that migratory flights are energetically cheaper than it is usually believed.
9. The departure decision is made by a migrant under the influence of many factors that may be lumped into four main groups. These groups of factors may be regarded as relatively independent and represented as orthogonal axes in the four-dimensional hyperspace: (1) current energy status; (2) habitat quality expressed as FDR; (3) weather conditions, mainly wind assistance; and (4) position on the migratory route with respect to the individual schedule of migration. In this hyperspace there exists a four-dimensional region where take-

offs are permitted. The more favourable the weather is the smaller fuel load is sufficient for departure. The more is a migrant delayed the more it is motivated to migrate, even in poor weather conditions and with low fuel stores.

8.7 Perspectives of Research of Stopover Ecology and Behaviour of Passerines

The proposed model of stopover behaviour (four-dimensional hyperspace) has to remain qualitative at the current stage of bird migration research. One of the main problems that hinders making this model a quantitative one is the problem of habitat quality quantification: it is only possible to express it through the fuel deposition rate for the individuals that remained, but not for the ones that left. Equally difficult is it to estimate the position of an individual on the migratory route with respect to its unknown individual migratory schedule, which defines the urge to migrate (the ‘pure’ motivation, free from the influence of habitat quality, fuel stores and weather conditions). Currently even the qualitative model seems to be a step forward in our understanding of the principles of organisation of migration in passerines.

The studies of stopover ecology and behaviour started in the late 1980s and intensively developed in the following two decades. Great progress was achieved in estimating stopover duration by capture-mark-recapture statistics and especially by radio-tracking of small passerines. Capture-mark-recapture modelling made it possible to estimate statistically correctly the duration of stopovers on the basis of biologically realistic assumptions. It should be emphasized that this method permits not only estimation of the *mean* stopover duration but also to study the structure of its variation which is most important for the understanding how flights and stopovers alternate.

Radio-tracking studies made it possible to obtain unbiased estimates of stopover duration and of spatial behaviour of migrants at stopovers. However, the problem of obtaining unbiased estimates of fuel deposition rate remains elusive. To understand the principles of organisation of stopovers and flights (i.e. organisation of avian migration) it is not sufficient to have unbiased estimates of the mean FDR across the stopover period, which is by itself very difficult. It is necessary to have daily estimates of FDR for each day of stopover *without* multiple captures and *without* supplementary feeding, which bias the estimates so much that make them useless. This aim remains to be achieved.

Further progress in this research will most probably be achieved by the transition from the ground-based to satellite telemetry of small songbirds. Such data might allow us to know exactly the beginning and the end of migratory flights of individuals with known body mass and energy stores. This opportunity may become available in the foreseeable future, if the ICARUS initiative, aimed at satellite tracking of small animals, including birds, with conventional small VHF transmitters, is realised (Wikelski et al. 2007; Robinson et al. 2010). Another avenue of research which is already open is using light–dark loggers, the so-called geolocators which make it possible to track the movements of small birds, including passerines, with the accuracy of 100–200 km (Stutchbury et al. 2009, 2011; Bächler et al. 2010; Heckscher et al. 2011; Ryder et al. 2011; Bairlein et al. 2012). Results of geolocator studies that have been published since several years have already brought a wealth of data on migratory speed, number and duration of stopovers, geographic aspects of migratory movements, and are beyond doubt a major factor of progress in avian migration research. Another serious advancement would be a possibility to weigh the free-living birds without capture and without supplementary feeding. It would permit to measure FDR and its variation with habitat, landscape, current energetic condition, weather etc.

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