Passerine Migration

Stopovers and Flight

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Chapter 2
Stopover Duration

Abstract In this chapter I describe and critically discuss the methods of estimating stopover duration. Potential pitfalls of the capture-mark-recapture analysis are discussed, and radio telemetry is recommended. However, an important benefit of capture-mark-recapture models is that they not only provide estimates of the mean stopover duration, but often allow studying within-species diversity of stopover strategies. The empirical results from the literature are reviewed. It is concluded that the duration of migratory stopovers of songbirds usually varies between 1 and 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, occasionally even longer. Significant proportions of migrants stop over for one day only and continue migration on the first night after arrival.

2.1 Methods of Estimating Stopover Duration

2.1.1 Minimum Stopover Length Estimates

Arguably, the most straightforward way to estimate stopover duration is to set up a trapping site, to capture stopping migrants, mark and try to recapture or resight them to read the marks. As most songbirds are inconspicuous, recaptures are used more frequently than resightings, even though it has been recently demonstrated that using both methods of encountering marked individuals significantly enhances the accuracy of stopover duration estimates as compared with using recaptures only (Salewski et al. 2007; Verkuil et al. 2010). The reason for this may be the fact that recapture probability does not remain constant throughout the stopover period, but generally declines towards its end (see below).

Large-scale capture-mark-recapture studies have become possible since the 1960s when mist-nets came into common usage for trapping birds. The simplest method to estimate the duration of migratory stopovers on the basis of

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capture-recapture data is the so-called *minimum stopover length*, *MSL*. Minimum stopover length (or duration) is time in days (or in hours) elapsed between the first capture of a bird and its last capture or resighting. As nocturnal migrants normally do not perform migratory flights during the daytime, their MSL is usually measured in whole numbers of days. Exceptions to this rule are the stopover durations of passerines that arrive after crossing a large water body (e.g. Gulf of Mexico; Gauthreaux 1971; Wang and Moore 1997), when flights may extend into the daytime and thus the first stopover day may not be a full one. It should also be noted that a nocturnal migrant that was only captured (once or multiple times) within a single day has a stopover duration of one, not zero days; a bird captured in two consecutive days has MSL = 2 days, etc.

When using MSL as a stopover duration estimate, it is assumed that time spent at stopover before the first capture and after the last capture is negligible. Even though under some circumstances this assumption may be justified (especially its former part), generally speaking, it is a very strong assumption. To know the true stopover duration, it is necessary to estimate its hidden part, i.e. time spent at stopover before the first capture and after the last capture or resighting. Therefore, MSL underestimates stopover duration, as apparent already from the word ‘minimum’. However, most authors only include birds captured at least twice in the analysis, and neglect individuals that were never recaptured (which are a vast majority in most cases). Obviously, this may lead to overestimates of the mean stopover duration. Therefore, MSL generally provides biased estimates, and it is even unclear whether these estimated are biased high or low.

2.1.2 Capture-Mark-Recapture Models: Estimating the Expected Stopover Duration

To solve this problem, it has been suggested that stochastic capture-mark-recapture models should be used that are common in animal demography studies (Lavée et al. 1991; Kaiser 1993, 1995, 1999). These models are used to estimate survival rates (Lebreton et al. 1992; Lebreton 2001; Burnham and Anderson 2002; Williams et al. 2002). They are used to compensate for imperfect capture probability. If all individuals present at the study site were captured every day with a 100% probability, we would have known their arrival and departure dates exactly and there would have been no reason to construct any models.

The main idea of this method is that all the birds present at the study site are considered to be an open population where all changes of numbers are due to immigration and emigration. Indeed, daily mortality rate at stopovers is usually low. On the basis of many individual capture histories (recorded as e.g. 10011011, where a 1 is a day when this individual was captured and 0 is a day when it was not captured) the daily apparent survival rate and daily capture probability are estimated. Capture probability (p) is the probability that a bird present at the study site is captured on a given day. Apparent, or local, survival rate (φ) is the probability that a bird present in the population on day i will be present on day $i + 1$. The local survival rate is the product of the true survival rate and the probability of staying in the study area. As the daily true survival rate is usually very close to 1, within the context of migratory stopovers φ is often called just the probability of stay. Emigration probability is $1 - \varphi$. Obviously, as both p and φ are probabilities, they vary between 0 and 1.

To identify the model that fits the data best (i.e. describes the dataset in the best possible manner), a number of models based on different assumptions are fitted. We may assume that φ, or p, or both parameters are time-dependent, i.e. within the context of migratory stopovers vary from day to day of trapping. Or we may assume that these parameters are time-independent, i.e. constant. Or they may vary between e.g. sex and age groups, or depend on the time elapsed since marking etc. All these models are theoretical ones and are based on our *a priori* knowledge of the ecology and behaviour of the animals studied. When many models are constructed, they are compared to find the most parsimonious one(s), i.e. the model(s) that explain the data best when using the smallest number of parameters. Models are usually compared by Akaike's Information Criterion (AIC) which is a measure of deviation of the model from the data, taking into consideration the number of parameters (Burnham and Anderson 2002). The model which fits the data best is the one that has the lowest AIC value (obviously, it depends on the models that we included into our comparison). The difference of a certain model from the best one is denoted as ΔAIC. In the best model $\Delta\text{AIC} = 0$ by definition.

It may happen that AIC values for two or several models are very similar, so that ΔAIC of some models is very low. This means that these models fit the data (nearly) equally well and it is difficult to say which one is better. In such case AIC weights are calculated that are probabilities of that the given model fits the data best. It is usually assumed that models with AIC weights >0.05 are worth considering. Usually AIC values are close in models with very similar structure. It suggests that the model structure is a correct one.

The expected stopover duration after the first capture is estimated as $S_a = -1/\ln \varphi$ (Seber 1982). This formula is a particular case of the following more general expression (Schaub et al. 2001):

$$S_a = (1 - \varphi_1) \cdot (-1/\ln \varphi_1) + \varphi_1 \cdot (1 - \varphi_2) \cdot (-1/\ln \varphi_2) + \varphi_1 \cdot \varphi_2 \cdot (1 - \varphi_3) \cdot (-1/\ln \varphi_3) + \cdots \quad (2.1)$$

when $\varphi = \text{const}$ (φ_1 is the probability of stay between the first and the second day; φ_2 between the second and the third day etc.).

Formula 2.1 makes it possible to obtain estimates of the expected stopover duration after the first capture. However, a bird may have arrived to the study site some time before the first capture and remained undetected. Therefore it is necessary to estimate this hidden stopover time before the initial capture. This is done by analysing the inverted capture histories when day 1 becomes day n, day 2, day n − 1 etc.; day n becomes day 1. From the inverted capture histories, seniority (γ) is estimated, which is the probability that a bird present in the population on day

i was also present on day $i - 1$ (Pradel 1996; Pradel et al. 1997). Immigration probability is $1 - \gamma$. Estimates of seniority allow calculation of stopover duration estimates before the first capture (S_b) similar to S_a calculation. The total stopover duration before and after the first capture is estimated as $S = S_a + S_b = (-1/\ln \varphi) + (-1/\ln \gamma)$ (Schaub et al. 2001).

It has been suggested that the term involving γ, i.e. S_b estimate, is superfluous and should not be included into the estimate of the total stopover duration (Efford 2005). It is so because presence at the time moment i is conditional on having not departed from arrival to i, but the birds that had arrived at e.g. $i - 2$ and departed before i are not included in calculations, biasing the estimate high. This is a matter of some debate (Efford 2005; Pradel et al. 2005), but most authors currently prefer not to include S_b into the total stopover duration estimate (Salewski et al. 2007; Bayly and Rumsey 2007; Chernetsov et al. 2007, Chernetsov 2010).

In practice this methodological problem is less severe than it looks. It has been mentioned before that in some cases the assumption that stopover migrants are captured quite soon after their arrival is justified. For instance, on the Courish Spit (south-eastern Baltic coast), like in many other coastal areas, passage has a pronounced wave-like pattern (Floerike 1893; Blyumental et al. 1967; Dolnik 1975; Titov and Chernetsov 1999). This wave-like pattern of passage influences stopover behaviour: periods with few individuals at stopover, many of which are captured repeatedly, alternate with peaks (or waves) of captures when many previously unmarked birds are trapped. It seems obvious that on the day of a wave of migration most freshly marked birds are new arrivals.

This intuitive idea is supported by our seniority analysis: on the first day of a migratory wave the probability that newly captured European robins *Erithacus rubecula* have been present at stopover earlier undetected is very low, as indicated by low seniority estimates. On a quiet day, i.e. during a pause between two peaks of captures, seniority is high (Table 2.1). It should be also kept in mind that the movement rate of stopover migrants, which governs capture probability to a large extent, is generally the highest during the first and sometimes the second day upon arrival and strongly declines afterwards (see Chap. 6).

A serious problem of using capture-mark-recapture models for estimating stopover duration is that this method is very data-hungry (Chernetsov and Titov 2000). Because of that, time-dependent models often have higher AIC values (e.g. lower support) than less sophisticated and often less realistic models with constant (time- and time-since-marking-independent) parameters. It happens because of overfitting, i.e. the number of parameters to estimate is too large for the number of capture histories available (Burnham and Anderson 2002). To solve this problem, data may be pooled, i.e. several days of trapping are treated as one capture event (Schaub and Jenni 2001a; Schaub et al. 2001). However, if more than one capture happens within this pooled capture event, information is lost. Moreover, data pooling has been shown to bias parameter estimates (Hargrove and Borland 1994; Morris et al. 2005b). To circumvent this problem, it has been suggested that the models should be fitted with the parameters fixed for several consecutive days (multiple day constancy models; Morris et al. 2005a). The number of parameters to

Table 2.1 Parameters of capture-mark-recapture models that describe stopover duration of European robins in Rybachy (Courish Spit, Eastern Baltic) in autumn 1996 (from Titov and Chernetsov 1999, revised)

Parameters		Mean estimate	95% confidence interval
Direct capture histories	φ_{11}	0.478	0.399–0.559
	φ_{12}	0.243	0.202–0.288
	φ_{13}	0.131	0.110–0.156
	φ_2	0.521	0.450–0.591
	φ_3	0.802	0.767–0.833
	p_1	0.266	0.237–0.297
	p_2	0.195	0.159–0.237
Inverted capture histories	γ_{11}	0.892	0.665–0.972
	γ_{12}	0.358	0.295–0.427
	γ_{13}	0.116	0.098–0.138
	γ_2	0.553	0.476–0.629
	γ_3	0.772	0.743–0.799
	p	0.236	0.212–0.262

estimate is reduced, as during data pooling, but the information on multiple captures within this time interval is not wasted. Therefore, using multiple day constancy models can be recommended when the data is scarce.

Another simple method to estimate the true stopover duration has been suggested by Vysotsky (1998). This method is based on the assumption that the first capture happens on average in the middle of stopover, and the last capture in the middle of the period between the first capture and departure. Therefore, MSL is on average 25% of the true stopover duration. Vysotsky's estimate is based on the implicit assumption that capture probability is constant throughout the period of stopover. This assumption ignores the known patterns of spatial behaviour at stopover (see Chap. 6) and is not justified. As all the capture methods used in standardised trapping projects are based on the passive capture of moving migrants, the capture probability is heavily dependent on the bird's mobility. The scale of movements strongly changes during stopover: it usually declines, often quite significantly (Chernetsov 2005; Chernetsov and Mukhin 2006).

2.1.3 Estimating the Proportions of 'Transients' and 'Non-Transients'

It should be emphasized that capture-mark-recapture models not only allow estimates of the mean expected stopover duration, but also to study the diversity of stopover strategies. As shown by our data (Chernetsov 1998b; Panov and Chernetsov 2010; Table 2.2; Sect. 2.4) and that of other authors (Salewski and Schaub 2007), the empirical data are often best described by a time-since-marking model (Cooch and White 2005), often called age-dependent models for brevity.

This usage originates from demographic studies where stochastic capture-mark-recapture models were initially developed and used and where capture events are often breeding seasons, so that the time since marking is often measured in years and thus shows the age of animals. In the context of migratory stopover ‘age’ is measured in days elapsed since the first capture.

Support of such models usually means that migrants that have just arrived with a high probability leave the stopover area after a one-day stopover (during the first night following arrival). The birds that stay for the second and even for the third day are likely to remain longer, usually for 5–8 days or more. In such situations it is justified to estimate the proportion of transients that make one-day stopovers and the mean expected stopover duration of non-transients, and not to pool both groups. The probability that a newly trapped individual is a transient (i.e. has a zero probability to remain longer than one day; Pradel et al. 1997) and stopover duration of non-transients is estimated from time-since-marking models. The probability that a fresh capture is a transient is calculated as $\tau = 1 - \varphi_1/\varphi_2$, where φ_1 is the probability of stay estimate in the first ‘age’ class (i.e. between the first and the second days of stopover), and φ_2 is the probability of stay estimate in the second class (between the subsequent days; Salewski et al. 2007).

Making distinction between transients and non-transients and estimating their stopover duration is not only justified by the formal logic of capture-mark-recapture modelling (Pradel et al. 1997; Salewski et al. 2007), but also by physiology-based motivation to continue migration (Rappole and Warner 1976; Tsvey et al. 2007). Certainly, strictly speaking, all migrants at stopover are transients, and it is not correct to call birds that just stay a little longer non-transients. However, making distinction between ‘transients’ (or ‘flyers’, birds that stop for one and sometimes two days) and non-transients (or ‘feeders’; Rappole and Warner 1976) that stay for a longer period is justified. This usage may be followed in order to keep capture-mark-recapture terminology uniform and mutually intelligible between different applications of this analysis.

2.1.4 Method of Elevated Mist-Nets

It should be emphasized that capture-mark-recapture models do not allow measurements of stopover duration of individual migrants. They only produce estimates of the mean expected stopover duration of cohorts of birds and confidence intervals of the means. However, in many cases it is essential to know the individual durations of stay. It is very difficult, nearly impossible, to observe the moment of arrival (but see Chap. 7). However, as mentioned above, on the first day of the peak of passage most trapped birds are indeed fresh arrivals (Table 2.1). High seniority values of migrants initially captured during the pauses of passage together with low seniority on the first day of migratory waves strongly suggest that birds first captured between the peaks of captures must have arrived with the previous wave of arrivals.

Fig. 2.1 Elevated mist-nets at the trapping site Rybachy on the Courish Spit. Photo by E. Popov

At the Biological Station Rybachy we have developed a method of capturing passerine nocturnal migrants during take-off in mist-nets set above the canopy (Fig. 2.1). It has been shown that captures in such nets that occur between 60 min after sunset and 60 min before sunrise do not refer to local movements that diurnal passerines do not perform in the darkness, as shown e.g. by the complete lack of their captures in standard ‘low’ mist-nets. Nocturnal captures in elevated, or ‘high’, mist-nets only refer to nocturnal migratory flights: take-offs, landing, or very low altitude migration (Bolshakov et al. 2000; Bulyuk 2006; Bulyuk and Tsvey 2006). When birds captured in nigh mist-nets have been previously marked (ringed) during their daytime stopover movements at the study site it is possible to claim that we exactly know the time of their migratory departure from stopover (Bolshakov et al. 2003a, b; Bulyuk and Tsvey 2006).

It should be mentioned that nocturnal trapping in high mist-nets is a very labour-consuming activity, especially because it is only useful when run in parallel with a large-scale daytime trapping project in the same area. In Rybachy, the project was run with more than 700 m of mist-nets checked hourly 24 h a day during seven autumn migratory seasons. It resulted in 78 documented migratory departures of European robins (the most common species; Bulyuk and Tsvey 2006) and lower number of captures of other songbird species. The minimum stopover duration of European robins varied between 1 and 12 days, on average 4.0 days (SD = 2.84, n = 78). However, if we disregard these additional, non-standard captures at take-off, and just analyse captures of the same individuals in the standard nets, their mean stopover duration would be estimated at 1.8 days (SD = 1.66), with variation between 1 and 9 days. The difference between these two estimates in individual birds is 0–10 days, or 0–91%, on average 46%. Apparently, this difference is too large to be ignored, and estimates based on recaptures in standard mist-nets are seriously low biased.

2.1.5 Radio-Tagging

The most objective method of estimating stopover duration is radio-tagging of migrants by small VHF transmitters. This method allows tracking of individual migrants until their migratory departure. Radio-tracking of passerines at migratory stopovers used to be hampered by the small size of the birds. Only in the 1990s, when small tags with a mass below 1 g became commercially available, radio-tagging studies of songbird migrants started to be published (e.g. Aborn and Moore 1997).

Lightweight transmitters used for tagging small (10–20 g) passerines usually have a limited signal strength and, as a result, not very large reception range, usually ca. 400–1,500 m depending on the habitat structure. Because of that, tagged birds that move even not very long distances may be lost. It should be kept in mind that even birds that normally remain within a rather limited home range during stopover, like European robins (Titov 1999a, b; Lajda 2001), may move for up to 1.5–2 km during the daytime (Chernetsov and Mukhin 2006). In order not to mistake such relatively long-distance diurnal movements for migratory departures, it is necessary either to do research on small islands where movement opportunities are limited (Aborn and Moore 1997; Schmaljohann et al. 2011), or to keep the birds under surveillance 24 h and to detect the moment of migratory take-off exactly (Chernetsov et al. 2004; Chernetsov and Mukhin 2006; Mills et al. 2011). This is especially important when species like e.g. the pied flycatcher *Ficedula hypoleuca* or garden warblers *Sylvia borin* are studied that are capable of moving for up to several kilometres during migratory stopovers (Chernetsov et al. 2004; Fransson et al. 2008). The point is that not every case when the signal from a tagged bird is no longer received from the ground can be automatically believed to indicate migratory departure. Exploratory flights or landscape-scale movements may result in the loss of signal (Schmaljohann et al. 2011; Mills et al. 2011).

One of the main strengths of radio telemetry is that detection probability of a bird is not dependent on its mobility. This makes telemetry studies radically different from capture-mark-recapture data when detection (recapture or resighting) probability is strongly dependent on spatial behaviour of migrants that may significantly change in the course of stopover. Therefore if the telemetry data is collected carefully, it should be regarded as the most accurate estimate of stopover duration. On the other hand, due to the high cost of transmitters as compared with rings, and due to labour intensity of ground-based telemetry (however, the advent of automatic receiving units helps to solve this problem) the sample size of radio-tagging studies will always remain more limited than in the ringing-based studies. Finally, as already mentioned, capture-mark-recapture statistics yields mean estimates for cohorts of birds and confidence limits for these estimates. Radio-tagging, like captures in elevated mist-nets, allows measurements of stopover duration of individual migrants.

2.2 Estimates Based on Re-Encounters of Marked Birds

2.2.1 Biased Estimates: Migratory Stopovers, Postfledging Movements, and Moult

The mean values of stopover duration estimates based on capture-mark-recapture data vary broadly. For instance, the stopover duration of Eurasian reed warblers *Acrocephalus scirpaceus* in Bolle di Magadino (Switzerland) was estimated as 12.25 days (SD = 1.67; n = 567) which is significantly longer than the MSL = 6.0 days (range 2–34 days, SD = 5.04; n = 108; Schaub et al. 2001).

These estimates deserve special attention. Duration of stay for 34 days in Central Europe can hardly refer to migratory stopovers. Beyond doubt they refer to the duration of stay of birds in juvenile moult that have not yet started autumn migration. Estimates of stopover duration during autumn passage are biased towards longer stopovers, especially in the Eurasian reed warbler, blackcap and other species with pronounced juvenile moult of body feathers (Jenni and Winkler 1994), because Schaub and Jenni (2000, 2001b) believe that autumn migration broadly overlaps with juvenile body moult. As supporting evidence these authors cited Herremans (1990) who tape-lured moulting Eurasian reed warblers at night in Belgium. However, Marc Herremans did not claim that the birds he captured were overlapping moult and autumn migration; he did not rule out that they were performing pre-migratory movements (juvenile dispersal).

Studies by Bulyuk et al. (2000) and Mukhin (2004) and Mukhin et al. (2005) clearly showed that juvenile Eurasian reed warblers performed nocturnal postfledging movements at the age of 36–50 days, i.e. before the onset of autumn migratory movements towards their winter quarters. The range of such movements is probably ca. several dozens of kilometres which is typical of juvenile dispersal distances of *Acrocephalus* warblers (Grüll and Zwicker 1981; Chernetsov 1998a; Paradis et al. 1998). These movements are not generally directed towards the winter quarters and are not migratory but postfledging movements of birds that are not in migratory disposition (Mukhin 2004; Mukhin et al. 2005). During these movements, Eurasian reed warblers and some other songbirds can be attracted by playback of conspecific and heterospecific song (Bulyuk et al. 2000; Mukhin et al. 2008). Therefore, the opinion that hatching-year Eurasian reed warblers broadly overlap juvenile moult and autumn migration in Central Europe is erroneous. Conversely, their long stays in the study sites (significantly longer in moulting individuals than in their conspecifics that have completed moult) found by Schaub and Jenni (2000, 2001b) strongly suggest that these are local birds in the broad meaning that are performing local postfledging movements and have not yet started autumn migration. Apparently, the inclusion of such birds in analysis biases stopover length estimates high (and FDR estimates low, see Chap. 3).

2.2.2 Reliable Capture-Mark-Recapture Estimates of Stopover Duration

Michael Schaub and Lukas Jenni estimated stopover duration of Eurasian reed warblers, sedge warblers *Acrocephalus schoenobaenus* and garden warblers at many sites from Finland to Spain and northern Africa by capture-mark-recapture models (Schaub and Jenni 2001a). The data were taken from the database of the European-African Songbird Migration Network (1994–1996; Bairlein 1995, 1998). For Eurasian reed warblers, I only used estimates for non-moulting individuals, since only they refer to the migrating birds (see above).

The mean stopover duration of Eurasian reed warblers was 3.7–7.7 days before the first capture and 3.1–6.1 days after the first capture (Table A1 in Schaub and Jenni 2001a; see Sect. 2.1.2 for the disputed usefulness of the estimates of stopover length before the first capture). Long stopovers (>10 days if the period before the first capture is included) were recoded on the Iberian Peninsula and in Morocco, and also in Bolle di Magadino (Switzerland) and on Lake Galenbeck in NE Germany.

Realistic estimates for the sedge warbler (as opposed to the obviously erroneous estimate for the Norwegian site, see above) are 1.8–12.0 days, obtained in Illmitz (E Austria), Rauvola (Finland), Rybachy (Kaliningrad Region), Lake Galenbeck and in Bolle di Magadino (0.9–6.3 days when only estimates after the first capture were included; Table A2 in Schaub and Jenni 2001a). In Illmitz the estimates varied between the years between 1.8 and 8.8 days. The authors suggest that such a broad annual variation was due to varying abundance of plum aphids *Hyalopterus pruni* that is believed to be the main food of sedge warblers in late summer and autumn (Bibby and Green 1981).

Garden warblers stopped for 3.4–14.1 days (1.7–7.1 days when only estimates after the initial capture are included; Table A3 in Schaub and Jenni 2001a). The very long estimate of 20.7 days refers to the total stopover duration in Ginak in Gambia which may refer to the wintering range rather than autumn passage.

It should however be emphasized that not all long stopovers should automatically be dismissed as unrelated to ‘true’ migration. This is shown by many estimates of stopover duration of passerine migrants that are facing ecological barriers and therefore need to accumulate significant fuel stores or have just crossed a barrier and need to recover.

Long-term data from a site just north of a major barrier are available from Eilat, an Israeli site on the northern tip of Gulf of Aqaba of the Red Sea. I analysed the

17-year data from 1984–2001 (except of 1987), and found that just 55 individuals stopped by at least two days (MSL), of 356 first captures. Of these 55 birds, only four were recaptured more than 10 days after the initial capture. However, in spring, after crossing the Sahara, 357 sedge warblers were recaptured at least one day after the first capture, 54 of them after at least 10 days. The maximum duration of stay in Eilat in spring was 46 days. Even if this stay referred to a sick or otherwise abnormal bird, durations of stay of 33, 35, 36 days probably represent the actual stopovers of sedge warblers during spring passage in Eilat. The body mass of these birds increased on average by 14.4%, whereas body mass increase in sedge warblers that stopped for 2–10 days comprised 7.3% (t-test, $t = 3.23$, $df = 314$, $p < 0.002$). Therefore, stopovers longer than 10 days are made by normal migrating sedge warblers, and not by sick or abnormal individuals. Eurasian reed warblers also make long stopovers in Eilat in spring, with MSL of up to 28 days. Of 270 individuals that stopped for more than one day, 27 remained for more than 10 days and increased their body mass on average by 12%.

Blackcaps stopped over in Eilat in spring for 3.54 days (males, $SD = 3.03$, $n = 386$) and for 3.86 days (females, $SD = 3.17$, $n = 526$), with significant sex-related difference in MSL (Mann–Whitney test, $U = 92460$, $p = 0.025$; Yosef and Wineman 2010). The maximum MSL was up to 35 days, i.e. similar to the values found in *Acrocephalus* warblers.

These estimates are made by the MSL method which has multiple methodological issues (Sect. 2.1.1). However, as we are here most interested not in obtaining unbiased estimates of the mean values (which is problematic by the MSL method), but in checking the validity of maximum estimates, the use of this method is justified in this case. It is also worth noting that these long stopovers were recorded during spring passage, when migrants are believed to be travelling fast because there is a high premium in arriving early to the breeding grounds (Kokko 1999, but see Forstmeier 2002).

Stopovers of Eurasian reed warblers before and after crossing the Sahara may be quite long, too. In autumn in Sidi Bou Ghaba near the Moroccan Atlantic coast adults stopped on average for 12.4 days, hatching-year birds for 17.8 days (capture-mark-recapture estimates with time before initial capture included; Rguibi-Idrissi et al. 2003). In Kerbacha on the Mediterranean coast of Morocco the values were 7.5 and 12.9 days, respectively. In spring the mean stopover duration estimates in Sidi Bou Ghaba were 8.1 days for adults and 13.5 days for yearlings; in Kerbacha the values were 3.2 days and 8.6 days, respectively. It should be however noted that ageing of Eurasian reed warblers during spring migration is not unproblematic.

Our estimates of the mean stopover duration in six species of passerine nocturnal migrants in Dzhanybek (northern part of the Caspian plain) varied between 0.85 days in the willow warbler to 3.4 days in the garden warbler in 2003 (Table 2.2). Even the upper limit of the 95% confidence interval did not exceed 5.7 (in the red-breasted flycatcher *Ficedula parva* in 2003)—5.8 days (in the garden warbler in 2003). It should be however, noted that unlike Schaub and Jenni (2001a) and Rguibi-Idrissi et al. (2003), we did not include stopover duration before initial capture in our estimates, following Efford (2005).

Table 2.2 Parameters of CMR models and stopover duration in songbird migrants in Dzhanybek (Western Kazakhstan)

Species, year	Proportion of transients	φ_1, mean and 95% confidence interval	φ_2 (or φ), mean and 95% confidence interval	Stopover duration, days (mean and 95% confidence interval)
Garden warbler 2003	0.58	0.313; 0.182–0.482	0.746; 0.620–0.841	3.41 (2.09–5.77)
Garden warbler 2004			0.572; 0.443–0.693	1.79 (1.23–2.73)
Common redstart 2003			0.576; 0.383–0.748	1.81 (1.04–3.44)
Common redstart 2004	0.80	0.139; 0.080–0.231	0.684; 0.575–0.776	2.63 (1.81–3.94)
Chiffchaff 2004			0.695; 0.564–0.800	2.75 (1.75–4.48)
Willow warbler 2004			0.307; 0.083–0.685	0.85 (0.40–2.64)
European robin 2004	0.65	0.215; 0.128–0.338	0.614; 0.424–0.774	2.05 (1.17–3.90)
Red-breasted flycatcher 2003			0.712; 0.540–0.839	2.94 (1.62–5.70)
Red-breasted flycatcher 2004	0.55	0.221; 0.109–0.396	0.490; 0.378–0.602	1.40 (1.03–1.97)

At the same site, in the spring of 2005 just two species of songbird migrants, the Blyth's reed warbler *Acrocephalus dumetorum* and garden warbler, were captured in significant numbers. The scarcity of recaptures did not allow estimates of stopover duration at spring passage, but the very fact that of 110 garden warblers marked in spring not a single bird was recaptured on subsequent days (in autumn this proportion was 43 out of 599, 7%) strongly suggests that the bulk of birds made one-day stopovers. Thus, after crossing the arid areas northwest of the Caspian Sea (garden warblers) and the deserts of Central Asia in spring (Blyth's reed warblers) migrants did not need to make prolonged stopovers to recover. A similar situation was recorded after spring crossings of the Gulf of Mexico (e.g. Wang and Moore 1993; Aborn and Moore 1997). It may be mentioned that MSL of garden warblers before crossing the Sahara in Amurum (Nigeria) in spring varied between 1 and 13 days, on average 5.0 days (SE = 1.15; n = 11, calculated from Fig. 5 in Ottosson et al. 2005).

In southern France the mean duration of migratory stopovers of Eurasian reed warblers varied between 6.1 days in late July and 11.1 days in late October, on average 8.5 days (Balança and Schaub 2005). This is very close to the estimates for this species at other European sites (Schaub and Jenni 2001a). In southern France the proportion of moulting Eurasian reed warblers was only 3.2% of all the captures (most probably these birds were completing moult); therefore the estimates seem to be realistic. It is worth nothing that stopover duration in this study significantly increased with the progress of season, whereas in the Eastern Baltic (Courish Spit) it did not change much, from 6.0 days in early and mid August to 8.1 in mid and late September (Chernetsov 1998b).

In northern Spain blackcaps stopped over on average for 9.6 days (SE = 0.6; Arizaga et al. 2008). Interestingly enough, in this study both the probability of stay (φ) and seniority (γ) were found to be related to arrival body mass. It resulted in a negative relationship between the predicted stopover duration and arrival body mass, with stopover length estimate varying between 3.6 and 13.6 days (for the fattest and the leanest individuals, respectively).

Our estimates of the mean stopover duration of European robins on the Courish Spit were much shorter, only 1.1 days after the first capture, or 2.3 days with the time before the first capture included (Titov and Chernetsov 1999). It should however be emphasized that these estimates average all birds, 'transients' and non-transients (see Sect. 2.4). The most adequate estimate of the stopover length of non-transients is the estimate for the birds initially captured during the pauses of migration, 5.7 days (Titov and Chernetsov 1999).

The mean stopover duration of bluethroats *Luscinia svecica* in northern Karelia was 4.24 days (95% confidence interval 3.73–4.77 days; Panov and Chernetsov 2010). Ca. 78% of adult bluethroats make a one-day stopover; the remaining 22% stop over for 4.24 days, like juveniles.

Stopover duration estimates of grasshopper warblers *Locustella naevia* in southern England made on the basis of multiple day constancy models (Morris et al. 2005a) varied between 1.35 (SD = 0.95) and 2.13 days (SD = 1.02) in different years. Interestingly, MSL estimates that took single captures into account were very close, from 1.18 (SD = 0.94) to 1.30 days (SD = 1.21; Bayly and Rumsey 2007).

Estimates of duration of autumn stopovers of songbirds on Appledore Island (Maine, US) based on multiple-day constancy models taking into account the time before the first capture varied in different years between 2.70 (SE = 0.56; n = 354) and 3.45 days (SE = 0.67; n = 189) in the red-eyed vireo *Vireo olivaceus*; between 2.92 (SE = 1.95; n = 141) and 3.81 days (SE = 2.62; n = 99) in the American redstart *Setophaga ruticilla*; between 4.84 (SE = 1.50; n = 153) and 6.84 days (SE = 8.54; n = 270) in the northern waterthrush *Parkesia noveboracensis* (Morris et al. 2005a).

2.2.3 Estimates Based on Resightings

Salewski et al. (2007) studied stopovers of songbird migrants during spring migration across the Sahara in Ouadâne, an oasis in central Mauritania. They not only recaptured stopover migrants after the initial ringing, but also searched for colour-ringed birds and thus resighted individually marked individuals. It generally resulted in more precise estimates of probabilities of stay and thus of stopover duration. The mean estimates of stopover duration were 7.55 and 9.49 days (two different years) for the subalpine warbler *Sylvia cantillans*; 4.02 and 7.43 days for the whitethroat *Sylvia communis*; 6.58 and 7.75 days for the orphean warbler *Sylvia hortensis*; 6.29 days for the willow warbler (calculated from the data presented in Salewski et al. 2007).

An interesting experimental approach to estimating stopover duration was used by Bayly (2006). This author recorded the presence of individually marked Eurasian reed warblers at a feeding table with mealworms during the postbreeding period and autumn migration in England. The birds were recorded without capture, thus the potential capture effect was avoided. Migrants that once started to use supplementary food, continued to do so. The author interpreted the disappearance of the birds as migratory departure. The duration of the refuelling period estimated by this method was on average 5.82 days (SE = 0.20; n = 38). The author excluded search/settling time from this period, i.e. time preceding efficient mass gain.

Trying to solve this problem, in another study this author estimated the total stopover time of sedge warblers by adding to the observed duration of visiting feeding tables the mean of two estimates of the duration of stay before the birds started visiting feeders (Bayly 2007). One estimate was based on the assumption that before appearing at the feeder the birds gained mass at the same rate as when using the feeder (which seems a rather unrealistic assumption—N.C.); the other, on the assumption that the FDR of these birds was the mean of the upper quartile of sedge warblers captured and recaptured in mist-nets that have not received supplementary feeding. This complex procedure based on many assumptions of doubtful validity was performed for the birds (their number is not reported) whose body mass at the moment of the first visit at the feeder exceeded the mean body mass of sedge

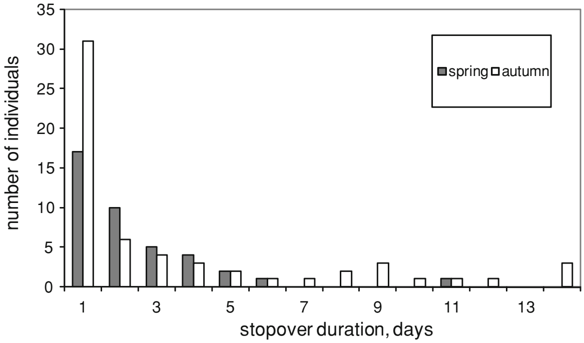

Fig. 2.2 Frequency distribution of stopover durations of radio-tagged European robins on the Courish Spit in spring (n = 40) and autumn (n = 59)

Table 2.3 Stopover duration of radio-tagged European robins on the Courish Spit on the Baltic coast in 2002–2003.

	Range of variation, days	Mean, days	Median, days	SE	Stopover > 2 days, %	n
Spring	1–12	2,4	2	0,31	30	40
Autumn	1–14	3,4	1	0,50	39	59

Only the birds tagged on the day of presumed arrival are included

warblers in that area by >1 g (Bayly 2007). The mean stopover duration estimated by this rather sophisticated method was 7.7 days (SE = 0.98; n = 20).

It should be noted that Bayly's experimental sedge warblers clearly formed two distinct clusters: those that stopped for 1–6 days (mean 3.8 days; SE = 0.47; n = 10) and gained mass up to 80% of the lean body mass at most; and those that stopped for 9–15 days (mean 11.6 days; SE = 0.69; n = 10) and gained 99–140% of the lean body mass. The sedge warblers from that latter group reached the body mass of more than 20 g and their FDR exceeded 13% per day which is at the very upper limit of the recorded FDR values (Bibby et al. 1976; Lindström 2003).

It should be also kept in mind that both Eurasian reed warblers (Bayly 2006) and sedge warblers (Bayly 2007) received supplementary food that allowed them to reach very high fuel deposition rates and may have very seriously influenced their stopover duration (see Chap. 4). These results might with some caution be used for studying the functional relationships between the stopover parameters, but should not be treated as the realistic estimates of stopover durations in the wild.

2.3 Estimates Based on Radio-Tagging

Radio-tagged European robins on the Courish Spit stopped for 1–11 days during spring migration, on average for 2.4 days (Fig. 2.2, Table 2.3). One bird that was not tagged on the first day upon arrival and because of that was not included into the analysis, stopped over for 12 days. Probably, 11–12 days is close to the upper limit of duration of spring stopovers of European robins.

In autumn, the stopover duration of European robins at the same site was 1–14 days, on average 3.4 days (Fig. 2.2, Table 2.3). The duration of migratory stopovers was not significantly different between the seasons (Mann–Whitney test, $z = 0.11$; $p = 0.92$). The autumn migratory stopovers of European robins on the Courish Spit were significantly shorter than in Mettnau on Lake Constance (SW Germany; 6.7 days, $SE = 1.04$; $n = 19$; Lajda 2001; Mann–Whitney test, $z = 2.79$; $p = 0.003$). Estimates from Mettnau are also based on radio-tagged birds, but in that study stopover duration might be biased high. Like in our study, wintering birds that have not left the study area before the end of study were excluded. However, the author did not follow nocturnal take-offs directly (Lajda 2001), therefore it cannot be claimed that all the individuals were indeed transient migrants at stopover. Some of them could have been wintering birds that changed their home range and were lost.

It is worth noting that the mean stopover duration estimated from telemetry data is very close to the estimate based on retrapping previously ringed birds in high mist-nets at the same site (3.3 days, calculated from the data in Bulyuk and Tsvey 2006).

We also radio tracked sedge warblers and pied flycatchers at stopover on the Courish Spit (Chernetsov et al. 2004). Of the 12 tagged sedge warblers seven stopped for one day, three for two and two for three days (mean 1.6 days, $SE = 0.23$). As pied flycatchers move at stopover significantly wider than sedge warblers or European robins (Chernetsov et al. 2004; Chernetsov 2005), it appeared possible to determine departure time in four individuals out of the seven tagged. The remaining three birds were lost during their diurnal movements, and we only have minimum estimates of their stopover duration, assuming that they took off on the night following their disappearance. Minimum estimates are that four birds made a one-day stopover, and two, three and four day stopovers were made by one individual each (mean 1.9 days, $SE = 0.46$).

Of 24 summer tanagers *Piranga rubra* radio-tagged during spring migratory stopovers immediately after crossing the Gulf of Mexico, 19 departed on the first night following arrival (i.e. made one-day stopovers), and five stopped over for more than one day (Moore and Aborn 1996). The exact stopover duration of these five birds remained unknown. It should be emphasized that even though summer tanagers were captured immediately after crossing the ecological barrier of at least 1,000 km of open water, 79% of them resumed migration on the first night upon arrival.

In a radio-tagging study of *Catharus* thrush stopovers at Long Point Bird Observatory on Lake Erie, Ontario, Canada, Swainson's thrushes *Catharus* *ustulatus* stopped over for an average of 3.4 days (up to 11.4 days) and hermit thrushes *C. guttatus* for an average of 8.9 days (up to 20.5 days; Mills et al. 2011).

Ovenbirds *Seiurus aurocapilla* radio-tracked in Brooklyn, New York City, in spring stopped over for 3.0 days on average (1–10 days, SE = 0.5, n = 27); 13 individuals made a one-day stopover (Seewagen et al. 2010). In autumn, they stopped over on average for 2.9 days (1–14 days, SE = 0.7, n = 22); 11 individuals departed in the first night upon arrival. All these values are very similar to the data from European robins on the Courish Spit.

A study of stopover duration of garden warblers on Crete in the eastern Mediterranean during autumn migration yielded very interesting results (Fransson et al. 2008). European robins, sedge warblers and pied flycatchers on the Courish Spit were studied during migration over optimal habitats; summer tanager stopped over immediately after crossing a barrier. Fransson et al. (2008) studied stopovers of migrants that were preparing for flights across half of the Mediterranean and the Sahara. The mean stopover duration was as long as 12.6 days (SE = 1.19; n = 20), and the authors do not rule out the possibility that birds tracked during 1–8 days were lost during local movements and did not embark on a migratory flight. If this is true, the stopover duration varied between 10 and 20 days, with the mean value of 15.3 days (SE = 0.63; n = 15). Thus, radio tracking data confirm the results of capture-mark-recapture studies in that before crossing major ecological barriers, passerine migrants make significantly longer stops than when migrating with a continuous stopover possibility.

2.4 Within-Species Variance in Stopover Duration: 'Transients' and 'Non-Transients'

Generally, stopover durations of 1–15 days are typical of small passerine nocturnal migrants that fly over ecologically suitable areas in Eurasia and North America with a continuous stopover opportunity. However, it is not always useful to estimate the *mean* duration of the stay of *all* migrants that make a stopover at a particular site. Not infrequently most birds stop for one day only. If a model with a time-since-marking-dependent probability of stay has the greatest support, some birds are transients with the probability of $\tau = 1 - \varphi_1/\varphi_2$. It was the case in Dzhanybek in western Kazakhstan (Chernetsov et al. 2007), in the Sahara (Salewski et al. 2007; Salewski and Schaub 2007), and, as our original data show, on the Courish Spit in the Eastern Baltic. During spring migration, in blackcaps the model that fitted the data best was φ (a2), p (.), i.e. with constant capture probability and time-since-marking-dependent probability of stay ($\varphi_1 = 0.146$; $\varphi_2 = 0.769$; $\tau = 0.81$). In whitethroats the best model was φ (a3), p (a2), i.e. with two time-since-marking classes of capture probability and three classes of probability of stay ($\varphi_1 = 0.175$; $\varphi_2 = 0.399$; $\varphi_3 = 0.838$; $\tau = 0.79$). In lesser whitethroats *Sylvia curruca*, a similar model received greatest support: $\varphi_1 = 0.161$; $\varphi_2 = 0.411$; $\varphi_3 = 0.855$; $\tau = 0.81$). In such situations it makes sense to estimate and to report the proportion of transients and stopover duration of non-transients. For example, in blackcaps on the Courish Spit the proportion of transients was 81%, the mean estimate of the stopover duration of non-transients was 3.81 days (–1/ln 0.769).

It has been suggested that all the birds that land after a migratory flight belong to one of the two groups: flyers, or transients, that are highly motivated to continue migration and therefore stop over for one or two days and feeders, or non-transients that mainly stop to refuel and thus intend to make a longer stopover (Rappole and Warner 1976). Stopover behaviour of the latter group is aimed at efficient foraging and refuelling which results in their search for optimal habitats and often competition-based interactions with conspecifics and heterospecifics (Rappole and Warner 1976; Dierschke and Delingat 2001). Usually or at least very frequently songbirds make several nocturnal migratory flights in a row (Fransson 1995; Bolshakov et al. 2003a, b; Hall-Karlsson and Fransson 2008). They make one-day stopovers between these flights, and a longer stopover when they complete such a series. As the aims of stopover in flyers and feeders are very different, their behaviour (foraging, spatial, and territorial) also may vary. However, to what extent the decision to continue migration in the next night after arrival is governed by the endogenous urge to migrate (i.e. is made even before arrival), and to what extent it depends on stopover events (habitat quality, food abundance, competition etc.) is a matter of debate. At least in European robins departure decisions are apparently governed by different environmental factors in birds that take off after short stopovers (1–2 days) and after longer stays with refuelling (Bulyuk and Tsvey 2006; Tsvey et al. 2007; Bolshakov et al. 2007).

It should be also kept in mind that estimates of the proportion of transients based on capture-mark-recapture data are usually seriously biased. It may happen if the range of daytime movements of migrants sharply declines some time after arrival at stopover. In such a case the proportion of birds that were captured within 1–2 days after their arrival can settle within a home range near the trapping site but outside of it. Some species do it regularly, as shown by our captures 500–1,000 m from the stationary trapping site. We repeatedly recaptured European robins and other migrants ringed at our trapping station beyond its borders. This is further supported by tracking of radio-tagged pied flycatchers (Chernetsov et al. 2004) and European robins (Chernetsov and Mukhin 2006). The proportion of radio-tagged European robins that departed from the study area on the Courish Spit on the first night upon arrival was much lower than the 87% suggested by capture-mark-recapture: 31 out of 59, i.e. 53% in autumn. In spring the proportion of one-day stopovers was even lower, 17 out of 40 (42.5%, Fig. 2.2). However, it is worth noting again that after crossing the Gulf of Mexico 79% of radio-tracked summer tanagers continued nocturnal migration on the first night after their arrival (Moore and Aborn 1996).

2.5 Concluding Remarks

Duration of migratory stopovers of songbirds usually varies between 1 and 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, occasionally even longer. 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.

Frequent occurrence of one-day stopovers means that many passerine nocturnal migrants make two or several nocturnal flights in succession, and then stop over for a longer period. It has been already suggested concerning several species of songbirds on the basis of analysing the distance of their flights from ringing data (Ellegren 1993; Fransson 1995) and fuel loads and potential flight range of birds captured during take-off and ceasing flight (Bolshakov et al. 2003a, b). The data on stopover durations support the existence of this pattern.

Such frequency distribution of stopover durations is reported from many regions. Except for areas before and immediately after ecological barriers, there are hardly any other unknown sites where nocturnal migrants gather for prolonged stopovers and refuelling. If most nocturnal migrants make several flights in a row, 'feeders' will always be a minority among the birds that arrive with a wave of migration. Certainly, it does not contradict the fact that some stopover sites are more suitable for refuelling than others, primarily because of varying habitat quality (Chap. 5; see also Ktitorov et al. 2008). Optimal migration theory predicts that stopover duration should be related to the fuel deposition rate (Alerstam and Lindström 1990; Lindström and Alerstam 1992; Hedenström and Alerstam 1997). Even though I criticise the optimal migration theory in Chap. 4, this statement seems to be correct. Fuel deposition rate is indeed one of the factors that govern stopover and departure decisions (Chap. 8).

References

Aborn DA, Moore FR (1997) Pattern of movement by summer tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. Behaviour 134:1077–1100

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E (ed) Bird migration. Springer, Berlin

Arizaga J, Barba E, Belda EJ (2008) Fuel management and stopover duration of blackcaps *Sylvia atricapilla* stopping over in northern Spain during autumn migration period. Bird Study 55:124–134

Bairlein F (1995) Manual of field methods, European-African songbird migration network. Institut für Vogelforschung, Wilhelmshaven

Bairlein F (1998) The European-African songbird migration network: new challenges for large-scale study of bird migration. Biol Cons Fauna 102:13–27

Balança G, Schaub M (2005) Post-breeding migration ecology of reed *Acrocephalus scirpaceus*, moustached *A. melanopogon* and Cetti's warbler *Cettia cetti* at a Mediterranean stopover site. Ardea 93:245–257

Bayly NJ (2006) Optimality in avian migratory fuelling behaviour: a study of a trans-Saharan migrant. Anim Behav 71:173–182

Bayly NJ (2007) Extreme fattening by sedge warblers, *Acrocephalus schoenobaenus*, is not triggered by food availability alone. Anim Behav 74:471–479

Bayly NJ, Rumsey SJR (2007) Grasshopper warbler *Locustella naevia* autumn migration—findings from a study in southeast Britain. Ring Migr 23:147–155

Bibby CJ, Green RE (1981) Autumn migration strategies of reed and sedge warblers. Ornis Scand 12:1–12

Bibby CJ, Green RE, Pepler GRM, Pepler PA (1976) Sedge warbler migration and reed aphids. Brit Birds 69:384–399

Blyumental TI, Gavrilov VM, Dolnik VR (1967) O prichinakh volnoobraznosti migratsii zyablika (On the causes of wave-like pattern of the chaffinch migration). Comm Baltic Comm Study Bird Migr 4:69–80

Bolshakov CV, Bulyuk VN, Sinelschikova A (2000) Study of nocturnal departures in small passerine migrants: retrapping of ringed birds in high mist-nets. Vogelwarte 40:250–258

Bolshakov C, Bulyuk V, Chernetsov N (2003a) Spring nocturnal migration of Reed Warblers *Acrocephalus scirpaceus*: departure, landing and body condition. Ibis 145:106–112

Bolshakov CV, Bulyuk VN, Mukhin A, Chernetsov N (2003b) Body mass and fat reserves of Sedge Warblers during vernal nocturnal migration: departure versus arrival. J Field Ornithol 74:81–89

Bolshakov CV, Chernetsov N, Mukhin A, Bulyuk VN, Kosarev V, Ktitorov P, Leoke D, Tsvey A (2007) Time of nocturnal departures in European robins, *Erithacus rubecula*, in relation to celestial cues, season, stopover duration and fat stores. Anim Behav 74:855–865

Bulyuk VN (2006) At what time of the day do passerine nocturnal migrants arrive at their breeding sites? Ardea 94:132–139

Bulyuk VN, Mukhin A, Fedorov VA, Tsvey A, Kishkinev D (2000) Juvenile dispersal in Reed Warblers *Acrocephalus scirpaceus* at night. Avian Ecol Behav 5:45–63

Bulyuk VN, Tsvey A (2006) Timing of nocturnal autumn migratory departures in juvenile European robins (*Erithacus rubecula*) and endogenous and external factors. J Ornithol 147:298–309

Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach, 2nd edn. Springer, NY

Chernetsov N (1998a) On the direction of postnesting dispersal in the sedge warbler (*Acrocephalus schoenobaenus*) (Passeriformes, Sylviidae). Russ J Zool 2:626–628

Chernetsov N (1998b) Stopover length and weight change in juvenile Reed Warblers *Acrocephalus scirpaceus* in autumn in the Eastern Baltic. Avian Ecol Behav 1:68–75

Chernetsov N (2005) Spatial behavior of medium and long-distance migrants at stopovers studied by radio tracking. Annals N Y Acad Sci 1046:242–252

Chernetsov N (2010) Migratory stopovers of wrens *Troglodytes troglodytes* on the south-eastern Baltic coast. Avian Ecol Behav 17:13–22

Chernetsov N, Bulyuk VN, Ktitorov P (2007) Migratory stopovers of passerines in an oasis at the crossroad of the African and Indian flyways. Ring Migr 23:243–251

Chernetsov N, Mukhin A (2006) Spatial behaviour of European robins *Erithacus rubecula* during migratory stopovers: a telemetry study. Wilson J Ornithol 118:364–373

Chernetsov N, Mukhin A, Ktitorov P (2004) Contrasting spatial behaviour of two long-distance passerine migrants at spring stopovers. Avian Ecol Behav 12:53–61

Chernetsov N, Titov N (2000) Design of a trapping station for studying migratory stopovers by capture-mark-recapture analysis. Avian Ecol Behav 5:27–33

Cooch E, White E (2005) Program MARK: a gentle introduction, 5th edn. http://www.phidot.org/software/mark/docs/book/. Accessed 28 Nov 2010

Dierschke V, Delingat J (2001) Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behav Ecol Sociobiol 50:535–545

Dolnik VR (1975) Migratsionnoye sostoyanie ptits (Migratory disposition of birds). Nauka, Moscow

Efford M (2005) Migrating birds stop over longer than usually thought: comment. Ecology 86:3415–3418

Ellegren H (1993) Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. Ornis Scand 24:220–228

Floerike C (1893) Vogelleben auf der Kurischen Nehrung. Ornithol Jahrb 4:1–11

Forstmeier W (2002) Benefits of early arrival at breeding grounds vary between males. J Anim Ecol 71:1–9

Fransson T (1995) Timing and speed of migration in North and West European populations of *Sylvia* warblers. J Avian Biol 26:39–48

Fransson T, Barboutis C, Mellroth R, Akriotis T (2008) When and where to fuel before crossing the Sahara desert—extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*. J Avian Biol 39:133–138

Gauthreaux SA Jr (1971) A radar and direct visual study of passerine spring migration in southern Louisiana. Auk 88:343–365

Grüll A, Zwicker E (1981) Nachbrutzeitliche Ortsveränderungen von Schilfrohrsänger (*Acrocephalus schoenobaenus*) und Teichrohrsänger (*A. scirpaceus*). Egretta 25:23–26

Hall-Karlsson KSS, Fransson T (2008) How far do birds fly during one migratory flight stage? Ring Migr 24:95–100

Hargrove JW, Borland CH (1994) Pooled population parameter estimates from mark-recapture data. Biometrics 50:1129–1141

Hedenström A, Alerstam T (1997) Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. J Theor Biol 189:227–234

Herremans M (1990) Body-moult and migration overlap in reed warblers (*Acrocephalus scirpaceus*) trapped during nocturnal migration. Gerfaut 80:149–158

Jenni L, Winkler R (1994) Moult and ageing of European passerines. Academic Press, London

Kaiser A (1993) Rast- und Durchzugstrategien mitteleuropäischer Singvögel, Analysen von Fang- und Wiederfangdaten von Fangstationen zur Beschreibung der Ökophysiologie und des Verhaltens rastender Populationen. Doktorarbeit, Universität Konstanz

Kaiser A (1995) Estimating turnover, movements and capture parameters of resting passerines in standardized capture-recapture studies. J Appl Stat 22:1039–1047

Kaiser A (1999) Stopover strategies in birds: a review of methods for estimating stopover length. Bird Study 46(Suppl):S299–S308

Kokko H (1999) Competition for early arrival in migratory birds. J Anim Ecol 68:940–950

Ktitorov P, Bairlein F, Dubinin M (2008) The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. Landsc Ecol 23:169–179

Lajda M (2001) Telemetrische Untersuchung zum Rastverhalten des Rotkehlchens (*Erithacus rubecula*) in Südwestdeutschland während des Herbstzuges. Diplomarbeit, Universität Zürich

Lavée D, Safriel UN, Meilijson I (1991) For how long do trans-Saharan migrants stop over at an oasis? Ornis Scand 22:33–44

Lebreton J-D (2001) The use of bird rings in the study of survival. Ardea 89:85–100

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

Lindström Å (2003) Fuel deposition rates in migrating birds: causes, constraints and consequences. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Heidelberg

Lindström Å, Alerstam T (1992) Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. Am Nat 140:477–491

Mills AM, Thurber BJ, Mackenzie SA, Taylor PD (2011) Passerines use nocturnal flight for landscape-scale movements during migratory stopover. Condor 113:597–607

Moore FR, Aborn DA (1996) Time of departure by summer tanagers (*Piranga rubra*) from a stopover site following spring trans-Gulf migration. Auk 113:949–952

Morris SR, Liebner DA, Larracuente AM, Escamilla EM, Sheets HD (2005a) Multiple-day constancy as an alternative to pooling for estimating mark-recapture stopover length in Nearctic-Neotropical migrant landbirds. Auk 122:319–328

Morris SR, Turner EM, Liebner DA, Larracuente AM, Sheets HD (2005b) Problems associated with pooling mark-recapture data prior to estimating stopover length for migratory passerines. In: Ralph CJ, Rich TD (eds) Bird conservation implementation and integration in the Americas: Proceedings of the 3rd International Partners in Flight conference 2002, USDA Forest Service General Technical Report PSW-191, Albany

Mukhin A (2004) Night movements of young reed warblers (*Acrocephalus scirpaceus*) in summer: is it postfledging dispersal? Auk 121:203–209

Mukhin A, Chernetsov N, Kishkinev D (2008) Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall. Behav Ecol 19:716–723

Mukhin A, Kosarev V, Ktitorov P (2005) Nocturnal life of young songbirds well before migration. Proc R Soc B 272:1535–1539

Ottosson U, Waldenström J, Hjort C, McGregor R (2005) Garden Warbler *Sylvia borin* migration in sub-Saharan West Africa: phenology and body mass changes. Ibis 147:150–157

Panov IN, Chernetsov NS (2010) Migratsionnaya strategiya varakushki (*Luscinia svecica*) v Vostochnoy Fennoskandii. Soobschenie 1: Osnovnye parametry migratsionnykh ostanovok (Migratory strategy of bluethroats, *Luscinia svecica*, in Eastern Fennoscandia. Part 1: Main stopover parameters). Proc Zool Inst 314:93–104

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J Anim Ecol 67:518–536

Pradel R (1996) Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics 52:703–709

Pradel R, Hines JE, Lebreton J-D, Nichols JD (1997) Capture-recapture survival models taking account of transients. Biometrics 53:60–72

Pradel R, Schaub M, Jenni L, Lebreton J-D (2005) Migrating birds stop over longer than usually thought: reply. Ecology 86:3418–3419

Rappole JH, Warner DW (1976) Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193–212

Rguibi-Idrissi H, Julliard R, Bairlein F (2003) Variation in the stopover duration of reed warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site. Ibis 145:650–656

Salewski V, Schaub M (2007) Stopover duration of Palearctic passerine migrants in the western Sahara—independent of fat stores? Ibis 149:223–236

Salewski V, Thoma M, Schaub M (2007) Stopover of migrating birds: simultaneous analysis of different marking methods enhances the power of capture-recapture analysis. J Ornithol 148:29–37

Schaub M, Jenni L (2000) Body-mass of six long-distance migrant passerine species along the autumn migration route. J Ornithol 141:441–460

Schaub M, Jenni L (2001a) Stopover durations of three warbler species along their autumn migration route. Oecologia 128:217–227

Schaub M, Jenni L (2001b) Variation of fuelling rates among sites, days and individuals in migrating passerine birds. Funct Ecol 15:584–594

Schaub M, Pradel R, Jenni L, Lebreton J-D (2001) Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. Ecology 82:852–859

Schmaljohann H, Becker PJJ, Karaardic H, Liechti F, Neaf-Daenzer B, Grande C (2011) Nocturnal exploratory flights, departure time, and direction in a migratory songbird. J Ornithol 152:439–452

Seber GAF (1982) The estimation of animal abundance and related parameters, 2nd edn. Macmillan, NY

Seewagen CL, Slayton EJ, Guglielmo CG (2010) Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecol 36:484–492

Titov N (1999a) Individual home ranges of Robins *Erithacus rubecula* at stopovers during autumn migration. Vogelwelt 120:237–242

Titov N (1999b) Home ranges in two passerine nocturnal migrants at a stopover site in autumn. Avian Ecol Behav 3:69–78

Titov NV, Chernetsov NS (1999) Stokhasticheskie modeli kak novy metod otsenki prodolzhitelnosti migratsionnykh ostanovok ptits (Stochastic models as a new method for estimating length of migratory stopovers in birds). Uspekhi Sovremennoi Biologii 119:396–403

Tsvey A, Bulyuk VN, Kosarev V (2007) Influence of energy condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behav Ecol Sociobiol 61:1665–1674

Verkuil YI, Wijmenga JJ, Hooijmeijer JCEW, Piersma T (2010) Spring migration of Ruffs *Philomachus pugnax* in Fryslân: estimates of staging duration using resighting data. Ardea 98:21–33

Vysotsky VG (1998) Prostoy sposob rasscheta istinnoy sredney prodolzhitelnosti ostanovki u migriruyuschikh ptits (A simple method of estimating the true mean stopover duration in migrating birds). Russ J Ornithol 52:3–19

Wang Y, Moore FR (1993) Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. Condor 95:934–943

Wang Y, Moore FR (1997) Spring stopover on intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263–278

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press, San Diego

Yosef R, Wineman A (2010) Differential stopover of blackcap (*Sylvia atricapilla*) by sex and age at Eilat, Israel. Naturwissenschaften 74:360–367