Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa

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Based on phenology, passage and median dates gathered from large number of study sites, we measured autumn and spring migration speeds of eleven long distance migratory passerines in four different eco-geographic sectors: Europe, desert, north eastern and eastern Africa. Results demonstrate that, during the southward autumn migration, late departing species, such as lesser whitethroat *Sylvia curruca*, garden warbler *S. borin*, spotted flycatcher *Muscicapa striata*, whitethroat *S. borin*, and willow warbler *Phylloscopus trochilus* cover their migration route with a slower average migration speed across Europe than do early migrating species. During spring migration, late departing species (marsh warbler *Acrocephalus palustris*, garden warbler, spotted flycatcher, red backed shrike *Lanius collurio*) across north eastern Africa showed a higher speed than early migrating species. Our results show overall shorter migration duration estimates in spring than autumn. Sector wise seasonal comparisons of duration indicate that migration journey in the African and desert sectors are covered in a relatively shorter time in spring than in autumn. Periods required to cover the distance between northern latitude breeding grounds and desert during both seasons were equivalent.

It is commonly accepted that birds modulate their migration with respect to time, energy and predation risk (Alerstam and Lindström 1990, Lindström and Alerstam 1992, Weber and Houston 1997, Weber et al. 1998, Alerstam 2003). In an optimal course of avian migration, all other factors being equal, time minimizing birds have the advantage of arriving at required wintering, moulting or breeding destinations earlier than competitors. Particularly in spring, where the breeding periods are short, time minimization could be crucial for reproduction. In such cases, evolution would favour an overall high migration speed that minimizes both flight and stopover time and thus facilitates early arrival at breeding locations.

High speed of migration could have critical fitness associated costs (e.g. reduced survival). Hence, not all species migrate at a high speed and different species commence migration at different times. Early departing birds might reach a required destination earlier than late departing species. This argument leads to the question of whether species that commence migration late migrate with a faster speed. Late departing species may not have to 'pace themselves' but might migrate with a faster speed for the entire migration (sprint) and arrive earlier or at least at an optimally comparable time with others.

Long distance migrating species that breed in the northern latitude and winter in tropical regions are exposed to different habitats and ecological conditions along their

migration routes. Migrating birds need to optimally modulate their travel costs and benefits of time, energy and safety according to specific ecological and geographical demands en route. Hence, migration speed might vary between different geographic sectors along the migration route.

In this study, we compared the speeds of migration in 11 passerine species during autumn and spring using speed estimates derived from the temporal patterns of migration (arrival and/or passage dates; Hildén and Saurola 1982, Ellegren 1990, Fransson 1995) along the eastern Africa migration route. The main objectives of the study are to compare the seasonal variation in the speed of migration in four different geographic sectors (Europe, desert, north eastern and eastern Africa) along the route and to measure the sector wise difference in migration speed between the different species depending on whether the species are on early or late schedule of migration. Based on total duration estimates, we also compared sector wise differences between spring and autumn migration speeds.

Methods

Data collection

Data for speed estimates were obtained from both published and unpublished sources on ringing sites (Fig. 1) and

Figure 1. Geographic distribution of study sites and migration sectors. Triangle, hexagon and square symbols indicate study sites in autumn, spring, and both autumn and spring, respectively.

migration studies in northeast and eastern Africa, particularly in Sudan (Nikolaus and Pearson 1982, Nikolaus 1983), Ethiopia (Ash 1980 and 1981, J. Ash unpubl. data, B. Biebach unpubl. data), Uganda (Pearson 1972 and unpubl. data, M. Fogden unpubl. data, M. Wilson unpubl. data), Kenya (Pearson and Backhurst 1976a,b and unpubl. data, Britton and Britton 1977 and unpubl. data), and Tanzania (L. and N. Baker unpubl. data, B. Biebach and U. Bauchinger unpubl. data). We considered data gathered from Egypt (Moreau 1961, Watson 1971, Goodman and Meininger 1989, B. Biebach and U. Bauchinger unpubl. data), Eritrea (Smith 1957), and Somalia (Archer and Godman 1961, Ash and Miskell 1998, J. Ash unpubl. data). We also used published and unpublished data sources from the Middle East and the Arabian regions. These include Israel (Safriel 1968, Safriel and Lavee 1988, Morgan and

Shirihai 1997), Jordan (J. Ash and R. Spencer unpubl. data, D. Pearson unpubl. data), Kuwait (Cleere et al. 2000 and unpubl. data), Oman and Saudi Arabia (G. Nikolaus, J. Ash, M. Evans and S. Newton unpubl. data). In addition, published migration information (e.g. Csörgö and Lövei 1995, Fransson 1995, Chernestov 1996, Lindström et al. 1996, Morgan and Shirihai 1997, Schmidt 1964, Bairlein 1997, Honza et al. 2000) were included in the analysis.

The species

The study focused on 11 species: the marsh warbler *Acrocephalus palustris*, sedge warbler *Acrocephalus schoenobaenus*, red backed shrike *Lanius collurio*, thrush nightingale *Luscinia luscinia*, nightingale *Luscinia megarhynchos*, spotted flycatcher *Muscicapa striata*, willow warbler *Phylloscopus*

trochilus, garden warbler *Sylvia borin*, whitethroat *Sylvia communis*, lesser whitethroat *Sylvia curruca* and barred warbler *Sylvia nisoria*. Selection of the species was based on (but not exclusively dependent on) Pearson et al. (1988), and Pearson and Lack (1992). Our main focus was to include trans Saharan migrants that migrate along the eastern African flyway/migration route (taken here as the route through Sudan, Ethiopia, Eritrea, Egypt, Somalia, Kenya, Uganda and Tanzania) with different spatio temporal migration patterns (Cramp and Perrins 1992 and 1993). The distinction between migratory and wintering birds was done according to the timing of migration described in Table 1. Some study sites in eastern Africa are also the wintering grounds for the species considered; hence in these locations both migrating and wintering birds might be present. The distinction between migratory and wintering birds was made according to the timing of migration described by Ash (1981), Pearson et al. (1988), Pearson and Lack (1992), Cramp and Perrins (1992 and 1993) and D. Pearson (unpubl. data), Table 1.

Data analysis

Migration speed estimates

Seasonal migration speeds were measured based on median passage and/or arrival dates of a species at given study locations along the migration route. Median dates were measured as dates when the cumulative ringing distribution passed 50% of the total capture in a given location. Migration speed estimates of individual species were calculated on the basis of "Population speeds". This estimate considers the distances travelled and time elapsed for a given species rather than an individual. Linear regression models were applied to the median dates of migrations, with distance as the dependent variable and time elapsed as the independent variable. Migration speeds were determined from a total data set comprising 128,833 birds in autumn and 29,625 birds in spring.

Migration speed estimates along geographic sectors

We compared migration speed for each species in different geographic regions by dividing the eastern flyway into four different sectors according to basic geographical and ecological conditions (Fig. 1). 1. European sector study sites located north of 40°N. 2. Desert localities in the Middle East and North Africa between 35°N and 15°N including Kuwait, Jordan, Israel, Saudi Arabia, Oman, Egypt, northern and central Sudan and Eritrea. 3. North eastern Africa (NE Africa) regions in the eastern African flyway located between 15°N and 0° equator (Central and southern Sudan, Ethiopia, Somalia, northern Kenya, northern and central Uganda). 4. Eastern Africa – localities between 0° equator and 10°S in southern Kenya, southern Uganda and Tanzania).

We then measured autumn and spring migration speed during the journey across the four ecogeographic sectors. Due to limited passage data during spring migration in Europe, we used median arrival date (as given by Cramp and Perrins 1992, 1993) at northern latitude breeding sites (north of 40°N) as a reference to estimate the speed between departure from the desert and arrival at breeding grounds. For some species and some migration sectors, median dates were reported from only two locations. In such cases, linear models could not be applied. Therefore, the speeds of migration were calculated by dividing the distance between the pairs of localities by the difference in median migration dates.

In brief, first we conducted a sector wise (Europe, desert, NE and eastern Africa) comparison of speed and analyzed the effect of timing and season on migration speed. Based on the sector wise speed estimates, we reconstructed the total duration of migration for each season. Duration was calculated from estimates of sector distances and the associated speed in the sector. Latitudinal sector distances were estimated to be 2,200, 2,000, 1,650 and 1,100 km for the Europe, desert, NE and eastern Africa sectors, respectively. We compared the difference between spring and autumn migration using seasonal sector wise total duration

Table 1. Earliest arrival (autumn) and departure (spring) dates considered (as defined in Methods) for each species at study sites in East Africa. The signs < and > indicate before and after, respectively, the dates given in the table.

Species	Study sites and migratory period (autumn (n), spring (n))				
	Ethiopia	Central Kenya	Uganda	Ngulia, Kenya	Tanzania
Marsh warbler	<Nov. 30 (53)	<Dec. 21 (108)		<Dec. 18 (40803)	<Jan. 30 (36) >Apr. 5 (45)
Sedge warbler	<Jan. 22 (40) >Apr. 15 (62)	<Dec. 27 (51) >Apr. 5 (689)	<Jan. 20 (92) >Mar. 7 (175)	<Dec. 21 (52)	
Red backed shrike	>Apr. 2 (63)	>Mar. 27 (63)	<Nov. 11 (77)	<Dec. 7 (1308)	>Mar. 11 (91)
Thrush nightingale	<Dec. 5 (173)	<Jan. 12 (59) >Apr. 20 (53)		<Dec. 15 (20686)	<Jan. 12 (32) >Mar. 14 (104)
Nightingale	<Nov. 29 (571) >Feb. 27 (63)			<Dec. 12 (346)	
Spotted flycatcher	<Dec. 5 (38) >Apr. 23 (135)				
Willow warbler	<Dec. 6 (60) >Mar. 25 (575)	<Dec. 20 (56) >Mar. 3 (1555)	<Dec. 17 (131) >Mar. 5 (89)	<Dec. 20 (1344)	<Dec. 25 (99) >Mar. 10 (751)
Garden warbler	<Nov. 25 (22) >Apr. 12 (209)	<Jan. 5 (73) >Mar. 25 (257)	<Dec. 20 (469) >Mar. 8 (320)	<Dec. 30 (469)	<Jan. 21 (210) >Mar. 10 (476)
Whitethroat	<Nov. 27 (249) >Mar. 15 (143)	<Nov. 25 (42) >Mar. 31 (265)		<Dec. 18 (22191)	<Dec. 25 (78) >Mar. 10 (401)
Lesser whitethroat	<Oct. 10 (97) >Mar. 5 (108)				
Barred warbler	>Mar. 12 (21)	>Mar. 21 (33)		<Dec. 18 (22191)	

estimates. Paired sampled t test was applied to compare variation between autumn and spring migration in each sector. Table 2 summarizes individual species passage date (covered in this study) across each geographic sector for both seasons.

Results

Autumn migration speed and median date showed a significant negative relationship in Europe ($r^2=0.70$, $P<0.001$, Fig. 2a) whereby later departing species cover their migration with slower average migration speeds. In spring, the average migration speed in NE Africa increased with the progress of the season ($r^2=0.75$, $P<0.01$, Fig. 3c). During the northward migration late migrating species, such as marsh warbler, red backed shrike, spotted flycatcher and garden warbler, all migrated at a faster speed than did early migrating species.

Sector wise comparisons between autumn and spring duration (paired t test) indicate that migratory journeys are covered in a much shorter time ($\pm$ SE) in spring than in autumn (Fig. 4) in the desert (autumn: 16.83 ± 0.93 vs. spring: 12.15 ± 0.79 , $n=8$, $t_7=14.77$, $P<0.01$), across Africa (NE Africa, autumn: 53.45 ± 8.93 vs. spring: 27.60 ± 6.39 , $n=8$, $t_7=2.20$, $P=0.04$ and East Africa, autumn: 52.17 ± 5.83 ; spring: 19.78 ± 12.25 , $n=7$, $t_6=5.49$, $P<0.01$). The time required to cover the distance in the northern latitude Europe for autumn and spring were equivalent (autumn: 20.20 ± 0.62 vs. spring: 22 ± 2.88 , $n=11$: $t_{10}=-0.58$, $P=0.55$).

Discussion

Results of this study indicate that along the sectors above 40°N , species migrating later in the autumn cover their

journey at a relatively slower average migration speed. These include species such as lesser whitethroat, garden warbler, spotted flycatcher, whitethroat and willow warbler. These findings are in agreement with the relationship of migration speed estimates and timing in Europe given by Alerstam and Lindström (1990). Several reasons have been proposed for the observed seasonal decline in speed including unfavourable and deteriorating environmental conditions such as shortened day length and food supplies (Alerstam and Lindström 1990, Ellegren 1993, Kvist and Lindström 2000, Hall and Fransson 2001, Alerstam 2003). In contrast, an increased migration speed in late migrants was observed during autumn migration in NE Africa for ($r^2=0.50$, $P=0.05$, Fig. 2c) particularly for sedge warbler and spotted flycatcher.

Selection for faster migration speed that minimizes time and maximizes early arrival at final wintering/moulting quarters might be stronger for long distance migrants heading to wintering grounds south of 10°N than most short to medium distance migrants, such as those bound for tropical winter quarters north of 10°N (e.g. lesser whitethroat). Particularly later in the season, the migration speed should accommodate a time to cover the remaining distance southward and time to undergo moult before commencing return migration. Early arrival at the wintering grounds can also play an important role in competition for high quality resources and establish winter territories (Lindström and Alerstam 1992).

Although with different statistical significance levels, relatively higher migration speed in late departing Palearctic passerines seems to be a general pattern in all sectors during spring migration. Birds migrate at an accelerated speed particularly in the northern latitudes after leaving NE Africa and while moving through the desert. Moreover, late migrants migrate at a higher speed than early migrating passerines. Since early arrival at the breeding ground can play a major role in competition for resources and

Table 2. Autumn and spring passage dates across each geographic sector.

Species	Geographic sector			
	Europe	Desert	NE Africa	Eastern Africa
Marsh warbler	8/18 9/21 5/9 5/25	8/26 9/24 5/6 5/17	9/7 11/22 5/1 5/7	11/22 12/29 4/12 5/7
Sedge warbler	8/10 9/5 4/25 5/8	8/31 9/7 4/29 5/8	11/25 12/11	12/5 12/19 3/30 4/26
Red backed shrike	8/29 9/15 5/6 5/26	9/7 9/15 4/28 5/6	4/2 4/28	11/18 11/24 4/4 4/24
Thrush nightingale	8/24 9/16	8/30 9/7 4/26 5/2	10/4 11/27	11/28 12/17 3/20 4/25
Nightingale			9/23 11/23 3/20 4/22	
Spotted flycatcher	3/20 4/16 8/27 9/16 5/7 5/26	4/6 4/22 9/8 9/16 5/1 5/16	10/18 11/30 4/26 5/1	
Willow warbler	8/27 9/5 4/25 5/13	9/3 9/15 4/25 5/2	10/20 11/7 4/22 4/28	11/8 12/12 3/19 4/24
Garden warbler	9/1 10/1 5/6 5/30	9/10 9/31 5/6 5/11	10/4 11/20 4/25 5/9	11/22 12/30 3/19 4/25
Whitethroat	8/28 9/15 4/25 5/16	9/7 9/15 4/24 5/4	10/11 11/8 3/21 4/26	11/9 12/12 3/16 4/9
Lesser whitethroat	9/3 9/23 4/6 4/29	9/12 9/23 3/30 4/24		
Barred warbler	8/15 9/8 5/5 5/31		3/19 4/26 3/15 4/20	3/21 4/21

Figure 2. Relationship between the autumn median migration date and average seasonal migration speed in Europe (a), desert (b), NE Africa (c) and eastern Africa (d) sectors.

reproduction (e.g. Lozano et al. 1996), selection for fast spring migration may be favoured. Higher migration speed in late spring migrants may be favoured by the rapid

increase in day length, hence longer fuel deposition times (Bauchinger and Klaassen 2005). Overall, the spotted flycatcher showed a characteristic migration pattern of

Figure 3. Relationship between the spring median migration date and average seasonal migration speed at breeding sites in Europe (a), desert (b), NE Africa (c) and eastern Africa (d) sectors.

Figure 4. Sector wise comparisons between autumn (a), and spring (b) migration duration. Average speed represents sector mean migration speed while cumulative time indicates average cumulative number of days required by the study species to migrate across each geographic sector. Arrows show seasonal migration directions.

relatively late departure but high speed in both autumn and spring (Figs. 2 and 3). Similarly, the marsh warbler showed a late departure but high speed migration strategy, particularly during spring. Most of the other species showed a varying departure time and speed of migration across the different sectors (Table 2).

Sector wise comparison of total duration indicates that birds migrate at a high autumn speed before reaching NE Africa followed by a lower speed and prolonged duration. One explanation for the lower migration speed in Africa is that several migratory species carry out moult between 8° and 11°N in NE Africa and interrupt migration. According to Pearson et al. (1988) and Jenni and Winkler (1994), most adults and a few juveniles of sedge warbler and whitethroat (mainly the race *icterops*) undergo partial moult and occasionally a complete moult. All adult marsh warblers undergo a partial body and primary moult before they resume migration to southerly located sites, where complete moult occurs. The two *Luscinia* species in this study also exhibit a rather extended stay in NE Africa.

The timing and speed of migration to the tropics and within the tropics follows a pattern that is synchronized with the successive availability of favourable conditions generated by seasonal climatic factors related to rainfall (Pearson 1990). Once the ecological barriers are crossed, passerines face relatively 'suitable' conditions and can afford a longer stopover and/or a slower journey. This may allow birds to minimize energy expenditure and predation risk. Thus, long distance tropical migrants may have been selected for maximizing migration speed in the first two sectors of

autumn migration before crossing the ecological barriers and for minimizing energy expenditure and predation risk during the second stage of their migration in Africa.

Sector wise seasonal comparison of migration duration indicates that migration journey in the African sectors and desert are covered in a much shorter time in spring than in autumn. These results support the general notation that migration speed is generally higher in spring than in autumn (Fransson 1995). Mean migration time between northern latitude breeding grounds and desert was nearly the same for both seasons. Similarly, Raess (2008) reported no significant difference between autumn and spring migration speed estimates for Siberian stonechats *Saxicola torquata maura* on migration across Central and northern Asia. Duration along this sector in the two seasons might be governed by different factors. Faster journey during autumn in Europe might be due to the need to cross the ecological barriers before food supplies and fattening conditions deteriorate. In spring, passerines migrants may fall under strict time pressure for timely arrival at the breeding grounds and with regard to competition for better quality breeding territories and mates (e.g. Kokko 1999).

Conclusions

The results of this study show that migration speed varies between different geographic sectors along the migration route, indicating that birds might optimally modulate their

migration speed according to specific ecological and physiological demands en route. Optimal migration speed that minimizes time dependent costs and risks associated en route, but enhances arrival at a required destination before competitors is essential for organizing birds' annual cycles. Migration speed that incorporates demanding migratory activities and other life history phases across varying geographic sectors might be an important factor in determining the migratory strategy and distribution of birds.

Generally, our migration speed measurements are in line with earlier studies on long distance passerine migrants given by Hyytiä and Vikberg (1973), Hildén and Saurola (1982), Hedenström and Pettersson (1987), Ellegren (1990, 1993), and Fransson (1995). However, in a study that compared spring and autumn speeds in five *Sylvia* species migrating using ringing recoveries across Europe, Fransson (1995) reported average ($\pm$ SEM) migration speeds of 91.6 ± 6.4 km/day and 138.0 ± 15.5 km/day in autumn and spring, respectively. Our population speed estimates in Europe differed from Fransson's (1995) individual speed values. Part of the explanation for the observed difference might be due to duration estimate biases from the ringing data we used. In autumn, we have used data points from individual birds trapped and ringed at bird observatories to measure median dates and 'population speed'. In spring, due to limited passage data available for each species, we have restricted estimates from median arrival dates at breeding grounds.

Theoretically, species specific life history strategies such as rate and frequency of annual moult and the migratory routes and distances, would regulate the migration speed in both seasons. Consistent with these concepts is that migration speed is regulated by an endogenous time program (Gwinner 1986, 1996a,b) that has been shaped by both spatial (e.g. Fransson et al. 2001) and temporal environmental factors, such as spatial distribution of suitable stopover areas and ecological barriers along the route (Terrill 1988).

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References

Alerstam, T. 2003. Bird migration speed. In: Berthold, P., Gwinner, E. and Sonnenschein, E. (eds). Avian migration. Springer Verlag, Berlin, Heidelberg, New York, pp. 253–267.
Alerstam and Lindström 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner, E. (ed.). Bird migration: physiology and ecophysiology. Springer Verlag, Berlin, pp. 331–351.

Archer, G. and Godman, E. M. 1961. The birds of British Somaliland and the Gulf of Aden, Vol. 3–4. Oliver and Boyd, London.
Ash, J. S. 1980. Migrational status of Palaearctic birds in Ethiopia. Proc. IV Pan Afr. Orn. Cong.: 199–208.
Ash, J. S. 1981. Bird ringing results and ringed bird recoveries in Ethiopia. *Scopus* 5: 85–101.
Ash, J. S. and Miskell, J. E. 1998. Birds of Somalia. Roberts bridge, U.K.
Bairlein, F. 1997. Spatio temporal course, ecology and energetics of western Palaearctic African songbird migration. Summary report 1994–1996. Institut für Vogelforschung, Wilhelmshaven.
Bauchinger, U. and Klaassen, M. 2005. Longer days in spring than in autumn accelerate migration speed of passerine birds. *J. Avian Biol* 36: 3–5.
Britton, P. L. and Britton, B. A. 1977. An April fall of Palaearctic migrants at Ngulia. *Scopus* 1: 109–111.
Chernestov, N. 1996. Preliminary hypotheses on migration of the sedge warbler (*Acrocephalus schoenobaenus*) in the eastern Baltic. *Vogelwarte* 38: 201–210.
Cleere, N., Kelly, D. and Pilcher, C. W. T. 2000. Result from late autumn ringing project in Kuwait, 1995. *Ring. & Migr.* 20: 186–190.
Cramp, S. and Perrins, C. M. 1992. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palaearctic. Vol. VI. Warblers. Oxford University Press.
Cramp, S. and Perrins, C. M. 1993. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palaearctic. Vol. VII. Flycatchers to Shrikes. Oxford University Press.
Csörgö, T. and Lövei, G. L. 1995. Autumn migration and recurrence of the thrush nightingale *Luscinia luscinia* at a stopover site in central Hungary. *Ardeola* 42: 57–68.
Ellegren, H. 1990. Autumn migration speed in Scandinavian bluethroats, *Luscinia s. svecica*, during autumn migration in Sweden. *Ring. & Migr.* 11: 121–131.
Ellegren, H. 1993. Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis. Scand.* 24: 220–228.
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., Jakobsson, S., Johannsson, P., Kullberg, C., Lind, J. and Vallin, A. 2001. Magnetic cues trigger extensive refuelling. *Nature* 414: 35–36.
Goodman, S. M. and Meininger, P. L. 1989. The birds of Egypt. Oxford University Press.
Gwinner, E. 1986. Circannual rhythms in control of avian migrations. *Adv. Study Behav.* 16: 191–228.
Gwinner, E. 1996a. Circannual clocks in avian reproduction and migration. *Ibis* 138: 47–63.
Gwinner, E. 1996b. Circadian and circannual clocks in avian migration. *J. Exp. Biol.* 199: 39–48.
Hall, K. S. S. and Fransson, T. 2001. Wing moult in relation to autumn migration in adult common whitethroats *Sylvia communis communis*. *Ibis* 143: 580–586.
Hedenström, A. and Pettersson, J. 1987. Migration routes and wintering areas of willow warblers *Phylloscopus trochilus* ringed in Fennoscandia. *Ornis Fenn.* 64: 137–143.
Hildén, O. and Saurola, P. 1982. Speed of autumn migration of birds ringed in Finland. *Ornis Fenn.* 59: 140–143.
Honza, M., Literák, I., Pavelka, J. and Formanek, J. 2000. Postbreeding occurrence of the marsh warbler *Acrocephalus palustris* in reedbed areas in the Czech Republic and its migration to Africa. *Ornis. Scand.* 22: 119–129.

- Hyttiä, K. and Vikberg, P. 1973. Autumn migration and moult of the spotted flycatcher *Muscicapa striata* and the pied flycatcher *Ficedula hypoleuca* at the Signilskär bird station. *Ornis Fenn.* 50: 134 143.
- Jenni, L. and Winkler, R. 1994. Moults and ageing of European passerines. Academic Press, London.
- Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* 68: 940 950.
- Kvist, A. and Lindström, Å. 2000. Maximum daily energy intake: it takes time to lift the metabolic ceiling. *Physiol. Biochem. Zool.* 73: 30 36.
- Lindström, Å. and Ålerstam, T. 1992. Optimal fat loads in migrating birds: a test of the time minimization hypothesis. *Am. Nat.* 140: 477 491.
- Lindström, Å., Hedenström, A. and Pettersson, J. 1996. The autumn migration of willow warbler *Phylloscopus trochilus* in Sweden: results from a nation wide co operative project. *Ornis Svecica* 6: 145 172.
- Lozano, G. A., Perreault, S. and Lemon, R. E. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *J. Avian Biol.* 27: 164 170.
- Moreau, R. E. 1961. Problems of Mediterranean Saharan migration. *Ibis* 103: 373 427.
- Morgan, J. H. and Shirihai, H. 1997. Passerines and passerine migration in Eilat. *Int. Birdw. Centr. Eilat. Tech. Publ.* 6: 1 50.
- Nikolaus, G. 1983. An important passerine ringing site near the Sudan Red Sea coast. *Scopus* 7: 15 18.
- Nikolaus, G. and Pearson, D. J. 1982. Autumn passage of marsh warblers *Acrocephalus palustris* and sprossers *Luscinia luscinia* on the Sudan Red Sea coast. *Scopus* 6: 17 19.
- Pearson, D. J. 1972. The wintering and migration of some Palaearctic passerines at Kampala, Southern Uganda. *Ibis* 114: 43 60.
- Pearson, D. J. 1990. Palaearctic passerine migrants in Kenya and Uganda: temporal and spatial patterns of their movements. In: Gwinner, E. (ed.). *Bird migration: physiology and ecophysiology*. Springer Verlag, Berlin, pp. 44 59.
- Pearson, D. J. and Backhurst, G. C. 1976a. The southward migration of Palaearctic birds over Ngulia, Kenya. *Ibis* 118: 78 105.
- Pearson, D. J. and Backhurst, G. C. 1976b. Palaearctic passerine migration at Kariobangi, Nairobi. *EANHS Bulletin* 1976: 23 28.
- Pearson, D. J. and Lack, P. 1992. Migration patterns and habitat use by passerine and near passerine migrant birds in eastern Africa. *Ibis* 134: 89 98.
- Pearson, D. J., Nikolaus, G. and Ash, J. S. 1988. The Southward migration of Palaearctic passerines through northeast and east tropical Africa: a review. *Proc. VI Pan Afr. Orn. Congr.*: 243 262.
- Raess, M. 2008. Continental efforts: migration speed in spring and autumn in an inner Asian migrant. *J. Avian Biol.* 39: 13 18.
- Safriel, U. N. 1968. Bird migration in Eilat, Israel. *Ibis* 110: 283 320.
- Safriel, U. N. and Lavee, D. 1988. Weight changes of cross desert migrants at an oasis do energetic considerations along determine the length of stopover? *Oecologia* 76: 611 619.
- Schmidt, E. 1964. Untersuchungen an einigen Holunder fressen den Singvögeln in Ungarn. *Zool. Abh. Mus. Tierkde. Dresden* 27: 11 28.
- Smith, K. D. 1957. An annotated check list of the birds of Eritrea. *Ibis* 120: 480 497.
- Terrill, S. B. 1988. The relative importance of ecological factors in bird migration. *Proc. XIX Int. Ornithol. Congr.*: 2180 2190.
- Watson, G. E. 1971. A serological and ectoparasite survey of migratory birds in northeast Africa. Smithsonian Institution, Washington.
- Weber, T. P. and Houston, A. I. 1997. A general model for time minimising avian migration. *J. Avian Biol.* 185: 447 458.
- Weber, T. P., Houston, A. I. and Ens, B. J. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. *Evol. Ecol.* 12: 377 401.

Appendix 1.

a) Autumn:

Country	Study site	Location			
Finland	Tauvo	64° 08'N, 24° 06'E	Uganda	Gaba	00° 06'S, 32°55'E
	Rauvola	60° 04'N, 22° 03'E		Kaazi	00° 12'S, 32°37'E
	Hanko	59° 08'N, 22° 09'E		Katalemiya	00° 38'S, 34°05'E
Sweden	Ottenby	56° 02'N, 16° 04'E		NW Elgon at Tegeres	01° 25'N, 34°25'E
Russia	Rybachy	55° 02'N, 20° 08'E		Lake Bisina	01° 35'N, 34°31'E
Germany	Galenbecker See	53° 06'N, 13° 07'E		Mweya/Lake Edward/	00° 10'S, 29°50'E
	Reit	53° 05'N, 12° 16'E		QENP	
Poland	Mierzeja Wislana	53° 03'N, 19° 03'E	Tanzania	Kifufu	03° 09'S, 39°12'E
Hungary	Budakeszi	47° 31'N, 18° 56'E		Mufindi	09° 05'S, 33°40'E
Ukraine	Taranqut	45° 57'N, 34° 14'E			
	Malachoni Liman	49° 35'N, 36° 47'E			
	Stephanovika	47° 53'N, 30° 53'E			
	Central Bulgaria	43° 00'N, 25° 00'E			
Sudan	Kho Barak	18° 03'N, 37° 30'E			
	K' Arbaat	19° 48'N, 37° 03'E			
	Wadihalfa	21° 50'N, 31° 25'E			
	Suakin	19° 06'N, 37° 18'E			
	Suakin Mangrooves	19° 02'N, 27° 23'E			
	Khartoum	15° 38'N, 32° 33'E			
	Sadat Farm	28° 30'N, 28° 55'E			
	Desert Station	29° 00'N, 29° 20'E			
Tanzania	Kikuru Reserve	01° 12'S, 31° 35'E			

b) Spring:

Country	Studysite	Location
Ethiopia	Debre Mariam Islands	13° 56'N, 39° 22'E
	Negele	05° 20'N, 39° 36'E
	Jijiga	09° 22'N, 42° 51'E
Jordan	Azraq	31° 49'N, 36° 49'E
Oman	Dauka	18° 40'N, 54° 04'E
	Salalh Sunfarm	17° 00'N, 54° 00'E
Egypt	Sinai/Israel	31° 08'N, 33° 25'E
Saudi Arabia	Farasan	16° 52'N, 41° 41'E
	El'Hair	24° 21'N, 46° 57'E
	Karan	24° 72'N, 49° 83'E

c) Autumn and Spring:

Country	Studysite	Location
Kuwait	Jahara	29° 19'N, 47°40'E
	Sulaibikhart	29° 18'N, 47°49'E
	Um Rimam	29° 55'N, 47°71'E
Israel	Eilat	29° 33'N, 34°57'E
Sudan	Kho Barak	18° 03'N, 37°30'E
Ethiopia	Abijata	07° 36'N, 38°40'E
	Bahadu	10° 11'N, 40°37'E
	Gambella	08° 15'N, 38°35'E
	Koka	08° 27'N, 39°06'E
	Aseita/Harar	11° 34'N, 41°27'E
	Didessa	09° 02'N, 36°09'E
	Bulcha	06° 27'N, 38°11'E
	Imi	06° 28'N, 42°10'E
	Afdem River	09° 30'N, 40°49'E
	Bosasso/Somalia	11° 16'N, 49°10'E
Kenya	Ngulia	03° 00'S, 38°13'E
	Karibangi NB	01° 15'S, 36°53'E
	Athi River	01° 26'S, 36°58'E
	Lake Nakuru	00° 20'S, 36°06'E
Kenya/Uganda border	Nyanza/Ng'iya/	00° 04'N, 34°22'E
	Lake Victoria area	