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Timing and speed of migration in North and West European populations of *Sylvia* warblers

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Timing and speed of migration within Europe and North Africa are analysed in five *Sylvia* warblers using North European and British ringing recoveries. Intraspecific comparisons between populations breeding in Great Britain and in Northern Europe show no difference in the timing of autumn migration but about three weeks earlier spring arrival in Great Britain, indicating that northern populations spend a shorter time on the breeding grounds. Autumn migration speed estimates based on distance and elapsed time between consecutive captures vary between 43 and 93 km d^{-1} depending on species and origin. High speeds of birds reported up to ten days after ringing suggest that some individuals have long flight-stages when they pass through Europe. Populations breeding in Northern Europe migrate at a higher speed than those in Great Britain. Shorter time on the breeding grounds and higher speed during autumn migration in more northern populations as well as higher speed in species undertaking longer migrations, indicate that migrants adjust their behaviour to a time shortage. Migration behaviour may thus be under selection to economize time. A compensatory increase in migration speed for late migrants, observed in some of the species, is consistent with the existence of such a selection pressure. Calculated spring migration speeds are higher than corresponding autumn speeds, but no obvious differences between northern and more southern populations are evident.

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Birds that carry out long-distance migrations have to deal with orientation and energy demands. During migration, individuals are affected by features like fattening, flight behaviour and habitat selection. Conceivably these behaviours are moulded by selection since long-distance migration is time-consuming and involves risks. The optimal solution will differ depending on the objective of the migrating bird. Migration strategies that minimize time, energy use or predation risk will have different influences on the behaviours involved (Alerstam and Lindström 1990). Patterns of migratory behaviour, such as migration speed, may thus provide cues to the selective forces that are operating.

Warblers within the genus *Sylvia* show great variation in migratory habits, both between and within species in different geographical areas (Berthold 1988a). Some species, like the Garden Warbler *S. borin*, are extreme long-distance migrants while other species breeding in southern Europe, such as the Sardinian Warbler *S. melanocephala*, are mainly resident (Moreau 1972, Zink 1973). In several of the *Sylvia* warblers, an endogenous annual rhythm has been shown to proximately regulate much of the migration pattern, including seasonally appropriate orientation and the length of the migratory periods (e.g. Berthold 1975, Gwinner and Wiltschko 1978, Berthold 1988b, Helbig et al. 1989). Migration routes of some European species and populations are well-known from ringing recoveries (e.g. Brickenstein-Stockhammer and Drost 1956, Rendahl 1960, Klein et al. 1973, Zink 1973, Langslow 1979, Fouarge 1981, da Prato and da Prato 1983, Jenni and Jenni-Eiermann 1987). In this study, recoveries of five species of *Sylvia* warblers (the Barred Warbler *S. nisoria*, the Lesser Whitethroat *S. curruca*, the Whitethroat *S. communis*, the Garden War-

Table 1. Median trapping dates during autumn and spring migration for five *Sylvia* species at Ottenby Bird Observatory (56°12'N 16°24'E), SE Sweden (data from Enquist and Pettersson 1986) and at Portland Bird Observatory (50°31'N 2°27'W), Dorset, Great Britain, 1975–91 (M. Rogers pers. comm.).

Species	Ottenby, Sweden				Portland, Great Britain			
	Autumn	n	Spring	n	Autumn	n	Spring	n
Barred Warbler	15 Aug	401	31 May	163				
Lesser Whitethroat	28 Aug	6613	21 May	6987	29 Aug	76	7 May	236
Whitethroat	19 Aug	4807	27 May	4994	28 Aug	586	7 May	688
Garden Warbler	1 Sep	3720	28 May	2592	27 Aug	870	10 May	965
Blackcap	21 Sep	1846	23 May	2002	13 Oct	1152	1 May	1962

bler and the Blackcap *S. atricapilla*) have been analysed in order to compare the timing and speed of migration within Europe and North Africa between species as well as between populations breeding in Northern Europe and at more southerly latitudes in Great Britain. With the exception of the Blackcap, the studied species are exclusively trans-Saharan migrants, of which the Garden Warbler migrates to the southernmost wintering area in Africa (Moreau 1972, Zink 1973). Blackcaps from Northern Europe and Great Britain have their wintering areas both in Central Europe, in the Mediterranean area, and in Africa south of the Sahara (Zink 1973, Langslow 1979, Fransson unpubl.).

Material and methods

Ringing recoveries from Norway (until 1987), Sweden (until 1991), Finland (until 1990), Denmark (until 1990) and Great Britain (until 1987) are analysed, making a total of 2353 recoveries at a minimum distance of 100 km between ringing and recovery sites. In this analysis, Norway, Sweden, Finland and Denmark are referred to as Northern Europe. Calculations of the average autumn migration speed (km d^{-1}), given as the arithmetic mean, are confined to recoveries at a minimum distance of 300 km, which approximately represents one night's flight. This limit excludes short distance movements, some of which probably are premigratory movements (cf. Langslow 1979, da Prato and da Prato 1983, Norman and Norman 1985). Only birds ringed and recovered during the same autumn migration period and recoveries from sites south of the ringing sites are included in these calculations. Because there is only one recovery from south of Sahara with these criteria fulfilled, calculations are confined to recoveries within Europe and North Africa.

The autumn migration period has been defined as 1 August–30 November for the Barred Warbler, Lesser Whitethroat, Whitethroat and Garden Warbler, and 20 August–30 November for the Blackcap, while the spring migration period for all species has been taken as 1 March–15 June from trapping figures at bird observatories (Enquist and Pettersson 1986, M. Rogers pers. comm.). Recovered birds were classified as naive (first autumn or spring migration) or experienced. Recoveries with uncertain information about dates or places have been excluded when the uncertainty affects the calculations. The distances between ringing and recovery sites were calculated according to the orthodrome (great circle), which is the shortest way between two sites (Imboden and Imboden 1972). Mean geographical positions (centres of gravity) were calculated according to Perdeck (1977), using his formula 2.

Median dates of trapping at two bird observatories, Ottenby (56°12'N 16°24'E) in Sweden (Enquist and Pettersson 1986) and Portland (50°31'N 2°27'W) in Great Britain (M. Rogers pers. comm.), have been used for data on the timing of migration in Northern Europe and in Great Britain, respectively. The timing of the passage across the Mediterranean area (29°N–45°N) has been calculated as median dates of recoveries in this area, irrespective of their longitudinal distribution. When calculating migration speed according to presence of birds at different latitudes, the time differences between the median dates of trapping at the bird observatories and the median dates for recoveries in the Mediterranean area were used. The distances used in these calculations refer to the distances between the bird observatories and the mean latitudinal position in the Mediterranean area of the recoveries from different species and regions.

Results

Timing of migration

The median trapping dates during autumn migration vary from 15 August in the earliest to 21 September in the latest species at Ottenby Bird Observatory, SE Sweden (Table 1). Spring migration is more concentrated in time. There is a mere ten-day difference between the earliest and the latest species (Table 1). In southern Great Britain (Portland Bird Observatory) the corresponding median dates during autumn are, with the exception of the Blackcap, similar to the dates found in Sweden (Table 1), while median trapping dates during spring are 2–3 weeks earlier (Table 1). The autumn trapping figures of Blackcap at Portland during 1975–91 have a secondary peak in Octo-

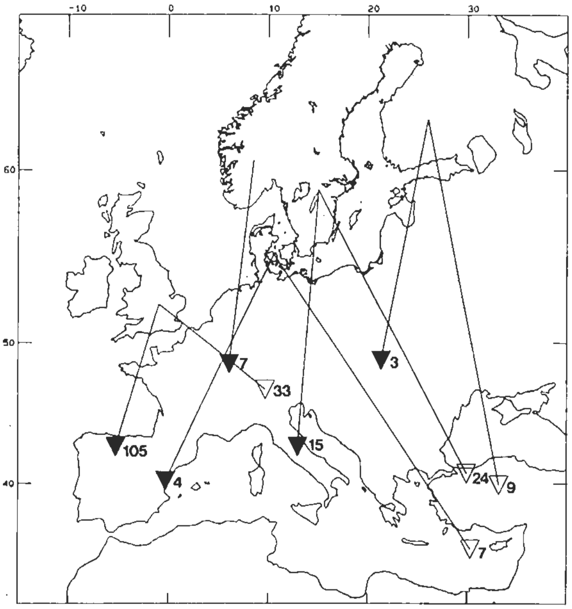


Fig. 1. Centres of gravity for recoveries reported during September from Lesser Whitethroats (open symbols) and Whitethroats (filled symbols) ringed in different countries. Lines connect the average position with the country of origin. Sample sizes are given beside each point.

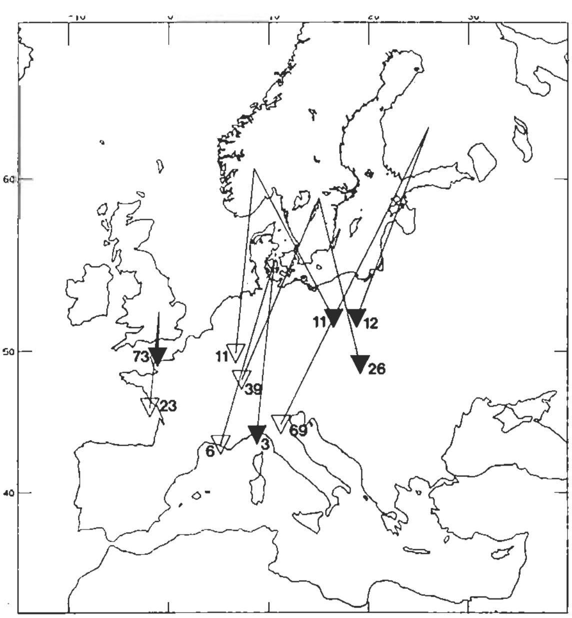


Fig. 2. Centres of gravity for recoveries of Garden Warblers (open symbols) and Blackcaps (filled symbols) reported during September and ringed in different countries (see Fig. 1 for explanation).

ber, also noted by Davis (1967), which may be attributed to birds originating from continental populations. The first peak is around 25 September and probably represents the median date for true British Blackcaps.

Mean geographical position for recoveries shows that in most cases the average positions for North European birds are at about the same latitude as for birds from Great Britain (Figs 1 and 2). There are, however, differences within species. Birds from Denmark are ahead of birds from other countries in all species (Figs 1 and 2). For the Lesser Whitethroat, all of which pass through the eastern Mediterranean area, the centres of gravity for September differ among populations. Birds from Northern Europe are on average close to the eastern part of the Mediterranean Sea while birds from Great Britain are on average in northern Italy (Fig. 1).

The median date for the autumn passage of the Mediterranean area varies from 14 September to 20 October (Table 2). The Barred Warbler and the Garden Warbler from Northern Europe are the earliest species and the latest species is the Blackcap. Usually there are small differences between birds from Great Britain and birds from Northern Europe. The median date for British Lesser Whitethroats is, however, about two weeks later than the corresponding date for birds from Northern Europe. Median dates for the spring passage of the Mediterranean area vary between 1 April and 13 May (Table 2). Whitethroats and Garden Warblers from Great Britain are about a week earlier than the birds from Northern Europe. In the Lesser Whitethroat the order of passage is the opposite to that in the autumn, and the median date of birds from Great Britain is about three weeks earlier than that of birds from Northern Europe. In contrast to the similar median dates for the autumn passage of the Blackcap, the spring passage of North European Blackcaps is about one month later than that of birds from Great Britain. The calculation of median dates for the Blackcap may be affected by the fact that they also winter in the Mediterranean area. With the exception of three birds, all of the included Blackcaps from Northern Europe were reported from the Middle East.

The autumn migration timing of different age-groups in Northern Europe (Ottenby Bird Observatory) shows both earlier (Garden Warbler) and later (Lesser Whitethroat and Whitethroat) departure in experienced than naive birds (Table 3). By separating the recovery material from the Mediterranean area into naive and experienced birds, sample sizes are reduced and calculations are not always possible. Autumn median dates of experienced birds are about one week earlier in the Lesser Whitethroat (1 Oct. (n=43) vs. 10 Oct (n=7), only birds from Northern Europe) and the Blackcap (GB: 15 Oct. (n=34) vs. 20 Oct. (n=31), NE: 7 Oct. (n=25) vs. 15 Oct. (n=22)) without being significantly different ($p > 0.05$, Mann-Whitney U-test). In the Garden Warbler, experienced birds have a much earlier median date than naive birds. This difference holds for birds from Great Britain (29 days; 20 Aug. (n=6) vs. 18 Sep. (n=10)) and from

Table 2. Median date for recoveries of five *Sylvia* species in the Mediterranean area (29°N–45°N) during spring and autumn migration. (GB = recoveries of birds ringed in Great Britain and NE = recoveries of birds ringed in Northern Europe.)

Species	Autumn				Spring			
	GB	n	NE	n	GB	n	NE	n
Barred Warbler			14 Sep	4				
Lesser Whitethroat	17 Oct	7	2 Oct	65	1 Apr	21	22 Apr	33
Whitethroat	21 Sep	119	25 Sep	26	30 Apr	12	10 May	9
Garden Warbler	29 Sep	21	15 Sep	82	3 May	12	13 May	9
Blackcap	20 Oct	74	17 Oct	59	10 Apr	54	6 May	49

Northern Europe (10 days; 10 Sep. (n=37) vs. 20 Sep. (n=23)). The difference is, however, only significant in birds from Northern Europe ($p<0.05$, Mann-Whitney U-test). In the Whitethroat, the median dates are reversed and median dates of experienced birds are later than for naive birds. This pattern is consistent, but not significant, for birds from Northern Europe (15 days; 27 Sep. (n=14) vs. 12 Sep. (n=8)) and birds from Great Britain (5 days; 23 Sep. (n=68) vs. 18 Sep. (n=40)). Spring migration median dates show both earlier passage (Lesser Whitethroats) and later passage (Blackcaps and in Garden Warblers from Northern Europe) in naive birds than in experienced birds, but neither of these differences is significant ($p>0.05$, Mann-Whitney U-tests).

Migration speed

The overall migration speed depends on both flying time and time spent at stopover sites. Migration speed is therefore overestimated from short-term recoveries, which include flight time but not a complete stopover cycle. Accordingly, speed estimates based on short-term recoveries declined with the elapsed time between ringing and recovery, with higher speed estimates in some individuals of up to about ten days (Figs 3 and 4). As more stopover time is included, the speed estimates start declining towards values which should represent average speeds over complete stopover cycles. The observed decline cannot be an effect of a selective loss of fast migrating individuals, because the Mediterranean area, at a distance of 2000 km and 3000 km for British and North European birds respectively, is not reached until after 30–40 days (Figs 5 and 6). It is also evident that birds reported after a longer time period have moved longer distances. A decrease in the speed estimates later on can be a combination of birds departing to sub-Saharan Africa with only the slowest individuals left and an increasing inaccuracy between the true and the reported finding date (Figs 3 and 4). In the case of Lesser Whitethroats from Great Britain (Fig. 4), the migration speed declines slowly up to about 40 days after ringing. Birds recovered from 40–60 days after ringing have a higher migration speed. This is probably due to birds taking off after making a longer stopover in northern Italy, about 1000 km from Britain (Fig. 6).

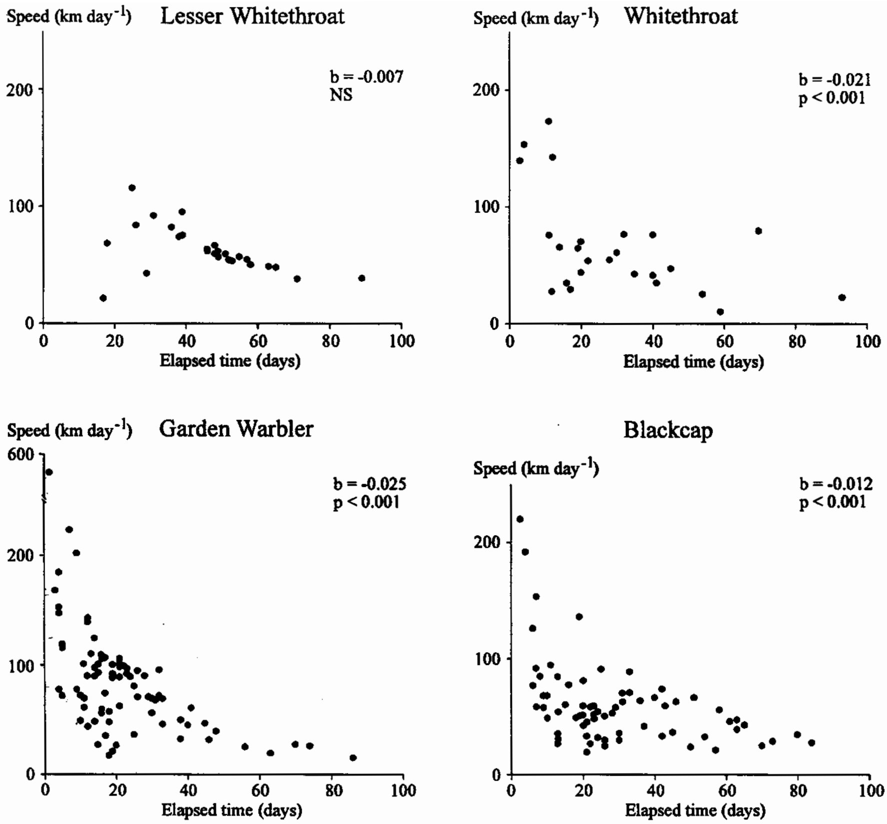
Table 3. Median trapping dates during autumn in naive and experienced birds of four *Sylvia* species at Ottenby Bird Observatory (56°12'N 16°24'E), SE Sweden 1978–90 (J. Pettersson pers. comm.).

Species	Naive Date	n	Experienced Date	n
Lesser Whitethroat	25 Aug	2100	3 Sep	143
Whitethroat	15 Aug	1305	5 Sep	86
Garden Warbler	30 Aug	1290	26 Aug	139
Blackcap	23 Sep	820	26 Sep	56

Because of the departure of birds to sub-Saharan Africa, the following calculations of migratory speed have been confined to recoveries made within 40 days of ringing. The average speed of autumn migration within Europe and North Africa in the different species varies between 43.4 and 62.3 km d^{-1} for birds ringed in Great Britain, while it is between 65.5 and 93.0 km d^{-1} for birds ringed in Northern Europe (Table 4). North European Lesser Whitethroats, Garden Warblers and Blackcaps migrate significantly faster than British conspecifics (Table 4). Migration is fastest for the Garden Warbler and slowest for the Blackcap and the Lesser Whitethroat. For British Lesser Whitethroats, the calculated average speed is clearly underestimated due to the stopover period in northern Italy. Comparisons of the average speed reveal no significant differences among species within geographical areas (one-way ANOVA, GB: $F_{3,114}=1.52$, $0.2<p<0.3$; NE: $F_{3,150}=2.52$, $0.05<p<0.1$). The results for North European *Sylvia* warblers come close to estimates for these and other long-distance passerine migrants from this region (Hyytiä and Vikberg 1973, Hildén and Saurola 1982, Hedenström and Pettersson 1987, Ellegren 1990, 1993).

A late start of migration may force individuals to migrate faster to reach their destination in time. There was a positive correlation between date of ringing and migration speed in all of the eight comparisons, however significant in only three of them (GB: Lesser Whitethroat $r_{16}=0.79$, $p<0.001$; Whitethroat $r_{44}=0.26$, $0.05<p<0.1$; Garden Warbler $r_{20}=0.36$, $0.05<p<0.1$; Blackcap $r_{38}=0.38$, $p<0.05$. NE: Lesser Whitethroat $r_{10}=0.28$, $0.4<p<0.5$; Whitethroat $r_{19}=0.55$, $p<0.05$; Garden

Fig. 3. The relationship between individual migration speed and elapsed time from ringing to recovery date for different *Sylvia* species ringed in Northern Europe (Norway, Sweden, Finland and Denmark).



Warbler $r_{71}=0.14$, $0.2<p<0.3$; Blackcap $r_{54}=0.21$, $0.1<p<0.2$).

Several studies suggest that the initial autumn migration speed is slower than the speed over longer distances (e.g. Hedenström and Pettersson 1987, Ellegren 1993). In this study, however, only British Garden Warblers and Blackcaps ($r_{20}=0.50$, $p<0.05$ and $r_{38}=0.52$, $p<0.001$ respectively) and North European Lesser Whitethroats ($r_{10}=0.84$, $p<0.01$) showed a significant positive relationship between migration speed and distance covered.

Average migration speeds estimated according to differences between median trapping dates in Northern Europe and Great Britain and median recovery dates in the Mediterranean area (Table 5) are generally higher than calculated from individual recoveries (Table 4). Even if these calculations may be affected by great uncertainty, estimates of autumn migration speeds are consistently higher in birds from Northern Europe than birds from Great Britain (Table 5). Based on information about median trapping dates for different age-groups during autumn migration at Ottenby Bird Observatory (Table 3) and median dates for different age-groups in the Mediterranean area, it is possible to calculate migration speeds for naive and experienced birds of the Lesser Whitethroat, Whitethroat, Garden Warbler and Blackcap from Northern Europe (Table 6). According to these estimates, experienced birds migrate faster by on average 24 km d^{-1}.

The spring migration speeds seem to be much higher than corresponding speeds during autumn and there is no clear difference in spring migration speed between birds from Northern Europe and Great Britain (Table 5).

Discussion

It is obvious that timing and speed of migration differ between species, between populations and between population cohorts. Which factors could account for these differences? Do different activities in the annual cycle compete for time so that timing and speed of migration are adaptively adjusted to different events?

Before migration can start, juveniles have to complete development (including postjuvenile moult), while adults have to complete breeding (including parental care) and moult (at least partial). Small differences in the onset of autumn migration and the up to three weeks earlier arrival during spring migration, indicate that birds breeding in Great Britain on average stay longer on their breeding grounds than do more northern birds. Populations and species with longer to go, migrate faster during autumn migration, with an average difference of 24 km d^{-1} between conspecifics from Northern Europe and Great Britain. Shorter breeding season and higher speed in more

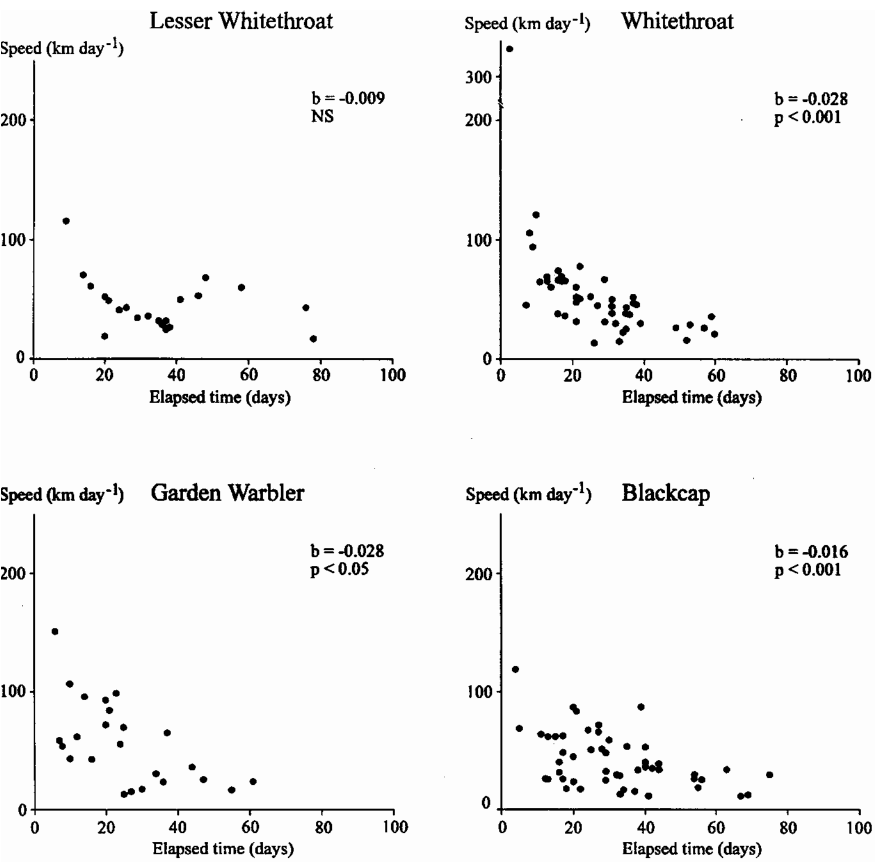


Fig. 4. The relationship between individual migration speed and elapsed time from ringing to recovery date for different *Sylvia* species ringed in Great Britain.

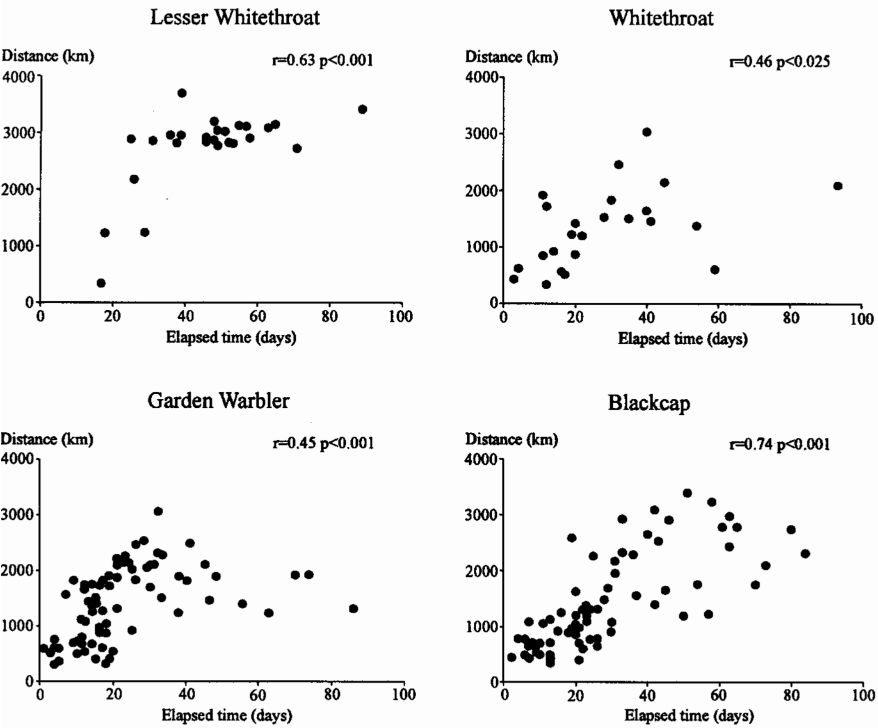
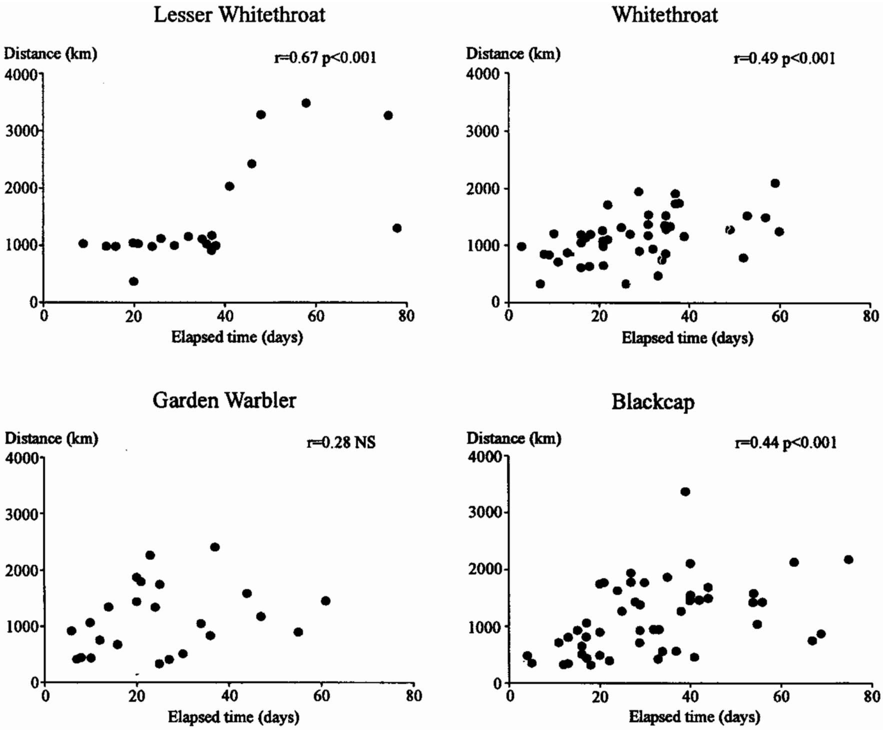


Fig. 5. Distance covered by *Sylvia* warblers ringed in Northern Europe (Norway, Sweden, Finland and Denmark) in relation to elapsed time from ringing to recovery date. Only recoveries more than 300 km from the place of ringing are included.

Fig. 6. Distance covered by *Sylvia* warblers ringed in Great Britain in relation to elapsed time from ringing to recovery date. Only recoveries more than 300 km from the place of ringing are included.



northern birds, together with higher speed in migrants with longer migrations, indicate that migrants are pressed for time and so migration speed may be under selection pressure.

The faster ontogenetic development in northern (Finnish) populations of the Garden Warbler (Berthold et al. 1974) is consistent with the notion of time stress and selection to gain time during the breeding season. An only partial post-nuptial moult may further enable adult birds to start migration shortly after breeding. The Garden Warbler is the only species of the five considered here that undergoes a complete moult in Africa instead of at northern latitudes (Ginn and Melville 1983). This difference in the moult of experienced birds coincides with the observed age-related variation in migration timing, where experienced Garden Warblers, in contrast to the other species, on average start migration before naive birds.

The average position of migrating birds in September and the timing of the Mediterranean passage show that North European birds catch up with, or are ahead of, British birds by the time they get to southern Europe. In the Garden Warbler, where northern populations move further south in Africa (Klein et al. 1973, Zink 1973, Dowsett et al. 1988), this is at variance with the theory that the more southern wintering grounds of northern populations is a result of asymmetric competition on the wintering grounds. This theory assumes that southern populations, by earlier arrival and occupancy of suitable habitats, force northern populations to move further south. This has been proposed to be an important force in shaping the winter distribution of different populations

Table 4. Autumn migration speed (mean ± s.e.) for four *Sylvia* species ringed in different areas of Europe. Only recoveries of birds recovered within 40 days after ringing, and birds recovered at a minimum distance of 300 km south of the ringing site have been used in the calculations.

Species	Great Britain		Northern Europe		p (t-test)
	Speed (km d^{-1})	n	Speed (km d^{-1})	n	
Lesser Whitethroat	43.4 ± 5.9	16	74.8 ± 8.5	10	< 0.01
Whitethroat	58.1 ± 7.0	44	75.0 ± 10.1	19	NS
Garden Warbler	62.3 ± 7.9	20	93.0 ± 8.4	71	< 0.01
Blackcap	46.7 ± 3.9	38	65.5 ± 5.2	54	< 0.01

Table 5. Speed of migration (km d^{-1}) in five *Sylvia* species from Northern Europe and Great Britain estimated according to differences in median trapping dates and median dates of recoveries in the Mediterranean area.

Species	Great Britain		Northern Europe	
	Autumn	Spring	Autumn	Spring
Barred Warbler			92	
Lesser Whitethroat	56	97	80	98
Whitethroat	47	186	85	129
Garden Warbler	39	232	116	163
Blackcap	52*	162	85	162

* Calculated according to an earlier median date (25 Sep) than is given in Table 4, see text for rationale.

(Lundberg and Alerstam 1986, Hedenström and Pettersson 1987).

Do birds, when migrating over favourable areas, accumulate fat for each night of flight, or do they normally accumulate fat which is used during several consecutive nights of flight? Some studies indicate that birds during migration have fat loads enough for several flight-nights and that these nights are separated only by short day-time stopover periods (Pettersson and Hasselquist 1985, Ellegren and Fransson 1992). In the *Sylvia* warblers studied here it seems probable that some individuals, when passing through Europe in autumn, cover considerable distances in short time periods. Such long flight-stages (including several nights of flying) suggest that they make use of stopover sites for longer periods. This disagrees with the average stopover time of 3–6 days found in several field studies (e.g. Dolnik and Blyumental 1967, Cherry 1982, Mehlum 1983, Bairlein 1985, Biebach et al. 1986, Veiga 1986, Loria and Moore 1990). It is also at variance with recent findings indicating that migrating birds in Europe often make short flights and use only part of the night for flight (Kaiser 1992, Ellegren 1993). Langslow (1976) found, however, that Blackcaps during autumn in Britain often stayed 7–10 days and that they increased their weights considerably. Migration time consists to a minor extent of flying time but mainly of time spent at stopover sites rebuilding energy reserves. Hence migration speed should be strongly affected by the fat deposition rate at stopover sites (cf. Alerstam and Lindström 1990). Assuming a flight speed of approximately 35 km h^{-1} in still air (Pennycuick 1975) and a hypothetical flight period of about 10 hours, a migrating bird will cover about 350 km during one night in still air. According to the calculated average migration speeds, one night of flying (350 km) will on average require between 3.8 and 5.3 days of stopover for North European birds, and 5.6 and 8.1 days for British ones. The average difference, within species, between birds from Northern Europe and Great Britain is 2.2 days. As differences should mainly be due to the time required to replenish energy reserves at stopover sites, this indicates that birds from Northern Europe accumulate fat faster than their conspecifics from Great Britain.

In some *Sylvia* warblers from Northern Europe and Great Britain, late individuals migrate at a higher speed than conspecifics migrating early during autumn. A compensatory increase in migration speed for late individuals suggests adaptations to a time stress. The reason for an increase in migration speed may be that there are several costs connected with a high speed (higher energy expenditure as well as greater predation risk due to increased foraging) and that late individuals may be more willing to pay these costs in order to improve their position within the population. Birds moving on after a short stopover period have to migrate with smaller energy reserves and smaller safety margins to gain time. Early birds may have a greater chance of obtaining territories on the wintering grounds (Price 1981). Adaptations to gain time are consistent with the suggestion that time-minimization (selection for fast migration) should be important in long-distance passerine birds as well as waders (Carpenter et al. 1983, Alerstam and Lindström 1990, Gudmundsson et al. 1991, Lindström and Alerstam 1992).

Data from Northern Europe show that experienced birds migrate faster than naive birds during autumn. In Bluethroats *Luscinia svecica*, naive birds have been shown to migrate at a slower speed during their initial phase of migration (Ellegren 1990). In this study, the speed of migration increased with distance covered in only three out of eight comparisons. Experienced birds may start migration either earlier or later than naive birds, depending on species. Hence, high speed in experienced birds is not necessarily a compensation for a late start. Conceivably, adults move fast because they are more experienced and better prepared, and not because they are short of time. Age-related differences in migration speed have been found in several other bird species (Saurola 1980, Ellegren 1993) and can be a result of experienced birds being able to accumulate fat at a higher rate than naive birds during stopover periods (cf. Veiga 1986).

The timing of the spring migration in different populations seems to be adapted to the phenology on the breeding grounds and the passage of the Mediterranean area shows that birds breeding in Great Britain migrate earlier than those from Northern Europe. The largest differences are found in the Blackcap and Lesser Whitethroat. Their later autumn passage and earlier spring passage, indicate

Table 6. Autumn migration speed (km d^{-1}) in naive and experienced birds of four *Sylvia* species from Northern Europe, estimated according to differences in median trapping dates at Ottenby Bird Observatory and median dates of recoveries in the Mediterranean area.

Species	Naive	Experienced
Lesser Whitethroat	61	101
Whitethroat	73	96
Garden Warbler	79	111
Blackcap	102	102

that British Lesser Whitethroats stay about one month less on the wintering grounds south of the Sahara than birds from Northern Europe. The available estimates of spring migration speeds are higher than those calculated for the autumn migration. Higher speed during spring migration, compared with autumn, has been shown in several species, for example Blackcap and Spotted Flycatcher *Muscicapa striata* (Fouarge 1981, Fransson 1985). No clear differences were found in the speed of spring migration between birds from Great Britain and from Northern Europe. Selection for fast spring migration may be equally strong in birds breeding in Great Britain and in Northern Europe, since an early arrival on the breeding grounds can be of great importance in competition for resources and for reproduction (cf. von Haartman 1968).

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