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. Intraspacific 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 45 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. Popula-
tions breeding in North 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 beha-

 jovices are moulded by selection since long-distance migra-

 tion is time-consuming and involves risks. The opti-

 mal 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. me-

 lanocephala, are mainly resident (Moreau 1977; Zink

 1973). In several of the Sylvia warblers, an endogeneous annal annual rhythm has been shown to proximately regulate much of the migration pattern, including seasonally ap-

 propriate orientation and the length of the migratory pe-

 riods (e.g. Berthold 1975, Owinsen 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. Brickensützer-Stockhol

 and Drost 1956, Rendahl 1960, Klein et al. 1973, Zink


 Prato 1983, Jennis and Jennis-Eermann 1987). In this

 study, recoveries of five species of Sylvia warblers (the

 Barred Warbler S. varius, the Lesser Whitethroat S.

 curruca, the Whitethroat S. communis, the Garden War-
### 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 2535 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 NOrwey. Calculations of the average autumn migration speed (km h⁻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. Lang-dow 1979, da Prato and da Prato 1983, Norman and Iorlano 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 Petterson 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 orthodromic (great circle), which is the shortest way between two sites (Inbo-den and Iab-den 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 Petterson 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 longitudinal 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 White-throats (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).

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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 toward 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 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 Ireland, about 1000 km from Britain (Fig. 6).

Because of the departure of birds to sub-Saharan Africa, the following calculations of migration 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戒指 in Great Britain, while it is between 65.5 and 93.0 km d⁻¹ for birds ringed in Northern Europe (Table 4). Northern 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 Ireland. Comparisons of the average speed reveal no significant differences among species within geographical areas (one-way ANOVA, GB: F₁,₉₅ = 1.52, 0.2 < p < 0.5, NE: F₁,₁₀₀ = 2.52, 0.05 < p < 0.1). The results for North European Sylviidae were close to estimates for these and other long-distance passerine migrants from this region (Hystil and Winkler 1973, Hiltan and Saarola 1982, Hedwhat and Petersson 1987, Elfen- gren 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 rₚ = 0.79, p < 0.001; Whitethroat rₚ = 0.26, 0.05 < p < 0.1; Garden Warbler rₚ = 0.36, 0.05 < p < 0.1; Blackcap rₚ = 0.38, 0.05 < p < 0.1). The results for North European Sylviidae were close to estimates for these and other long-distance passerine migrants from this region (Hystil and Winkler 1973, Hiltan and Saarola 1982, Hedwhat and Petersson 1987, Elfen- gren 1990, 1993).
Wabler $t_{12} = 0.14, 0.2 < p < 0.3$; Blackcap $t_{12} = 0.21, 0.1 < p < 0.2$.

Several studies suggest that the initial autumn migration speed is slower than the speed over longer distances (e.g. Hedstroem and Peterson 1987, Ellegren 1993). In this study, however, only British Garden Warblers and Blackcaps ($t_{12} = 0.50, p < 0.05$ and $t_{12} = 0.52, p < 0.001$ respectively) and North European Lesser Whitethroats ($t_{12} = 0.84, p < 0.001$) 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 Ongley 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 than the average 24 km d$^{-1}$.

The spring migration speed seems 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 populations. 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 molt), while adults have to complete breeding (including parental care) and molt (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 conspecific 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 Syliva species ringed in Great Britain.

Fig. 5. Distance covered by Syliva 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.
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 (Flanaghan) 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-natal molt 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 molt in Africa instead of at northern latitudes (Gunn and Melville 1983). This difference in the molt 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Great Britain</th>
<th>Northern Europe</th>
<th>p (t-test)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Speed (km d⁻¹)</td>
<td>n</td>
<td>Speed (km d⁻¹)</td>
</tr>
<tr>
<td>Lesser Whitethroat</td>
<td>43.4 ± 5.9</td>
<td>16</td>
<td>74.8 ± 8.5</td>
</tr>
<tr>
<td>Whitethroat</td>
<td>58.1 ± 7.0</td>
<td>44</td>
<td>75.0 ± 10.1</td>
</tr>
<tr>
<td>Garden Warbler</td>
<td>62.3 ± 7.9</td>
<td>20</td>
<td>93.0 ± 8.4</td>
</tr>
<tr>
<td>Blackcap</td>
<td>46.7 ± 3.9</td>
<td>38</td>
<td>65.5 ± 5.2</td>
</tr>
</tbody>
</table>

(Lundström and Ålerstam 1986, Hedenström and Potters-
son 1987).

Do birds, when migrating over favourable areas, accu-
mulate 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 (Petterson and Hasselquist 1985, Elle-
gren and Fransson 1992). In the Sylvia warblers studied
here it seems probable that some individuals, when pass-
ing through Europe in autumn, cover considerable dis-
tances in short time periods. Such long flight-stages (in-
cluding 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 sever-
Al field studies (e.g. Dostnik and Biljumsental 1967,
Cherry 1982, Mehlman 1983, Balint et al. 1986, Viega
1986, Loria and Moor 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

Langslow (1976) found, however, that Blackcaps in
autumn in Britain often stayed 7-10 days and that they
increased their weights considerably. Migration time con-
sists to a great 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. Ålerstam and Lind-
ström 1990). Assuming a flight speed of approximately
35 km h \(^{-1}\) in still air (Pennycuick 1975) and a hypotheti-
cal flight period of about 10 hours, a migrating bird will
cover about 350 km during one night in still air. Accord-
ing 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. 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 com-
mensurate 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 expen-
diture 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 con-
sistent with the suggestion that time-minimization (selec-
tion for fast migration) should be important in long-
distance passerine birds as well as waders (Carpenter et
al. 1983, Ålerstam and Lindström 1990, Gudmundsson et

Data from Northern Europe show that experienced
birds migrate faster than naive birds during autumn. In
Blauhøna Luscinia svecica, naive birds have been shown
to migrate at a slower speed during their initial phase
of migration (Ellerig 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, birds move faster 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 (Swanson
1980, Ellerig 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. Viega 1986).

The timing of the spring migration in different popula-
tions seems to be adapted to the phenology on the breed-
ing grounds and the climate of the Mediterranean area.
Birds in the Mediterranean area 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>
<thead>
<tr>
<th>Species</th>
<th>Naive</th>
<th>Experienced</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lesser Whitethroat</td>
<td>61</td>
<td>101</td>
</tr>
<tr>
<td>Whitethroat</td>
<td>73</td>
<td>96</td>
</tr>
<tr>
<td>Garden Warbler</td>
<td>79</td>
<td>111</td>
</tr>
<tr>
<td>Blackcap</td>
<td>102</td>
<td>102</td>
</tr>
</tbody>
</table>

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

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 (Fouqué 1981, Franckson 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 they arrive on the breeding grounds can be of great importance in competition for resources and for reproduction (cf. von Haartman 1968).

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