

## How far do birds fly during one migratory flight stage?

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Birds on migration normally switch between flight stages and periods of stopover where fuel stores are replenished. How migratory birds divide their time between flight and stopover is still not well known. Short-term recoveries of passerine birds ringed in Sweden were analysed to investigate how far long-distance migrating passerines fly during a flight stage and whether they migrate one or more flight stages in a row. Included in the study were birds recovered at least 50 km from the ringing site and within seven days from ringing. The median distance covered by the recovered birds was 245 km. About 40% of the recoveries within 24 hours from ringing were found at least 200 km from the ringing site. The distances covered varied and many birds moved only short distances, perhaps as a result of searching for good stopover sites, while others moved much further away. Two recoveries of Sedge Warblers three days after ringing indicated that these birds had flown three nights in a row before being controlled. The results suggest that long-distance passerine migrants regularly perform several flight stages in a row, with short rests in between, before refuelling, even if there are no major barriers ahead.

The speed of migration in birds has been the focus of several studies. The study methods used are diverse and range from analyses of recovery data of ringed birds (cf Hildén & Saurola 1982, Ellegren 1993, Fransson 1995, Bensch & Nielsen 1999) to radar studies (cf Bloch & Bruderer 1982) and mathematical modelling (cf Schaub & Jenni 2001, Schaub *et al* 2008). These studies have, for example, led to the conclusions that passerine birds on migration fly at most around 200–300 km/d (Hildén & Saurola 1982) and that nocturnal migrants, on average, travel faster than diurnal migrants (Hildén & Saurola 1982). Ellegren (1993) found that the average flight length for nocturnal migrants was significantly longer than for diurnal migrants. Also, the speed of migration has been shown to be higher for individuals ringed later in the season and to differ between species (Fransson 1995, Bensch & Nielsen 1999).

During migration, birds switch between flight and periods of stopover. Migration speed depends on flight speed as well as on time spent on stopover sites (cf Fransson 1995). The maximum speed estimates from field data have been suggested to relate to birds flying during favourable weather conditions or crossing areas without suitable stopover places (Hildén & Saurola 1982). The average migration speed over longer distances is, by definition, lower than the maximum migration speed because of the inclusion of stopover time. A bird on migration might have to choose between minimizing time, energy or predation risk

(Alerstam & Lindström 1990). If minimizing predation risk is most important, fuel load should be as low as possible, since flight performance will be affected by a higher body mass (Hedenström 1992). If minimizing energy expenditure is the goal, the most efficient way to migrate would be to fly only one day or night in a row and carry around no more fuel than necessary for the distance to be covered. If food availability is good all along the route and food sources are predictable and not clumped this might be a good strategy, but species fuelling from clumped or unpredictable food sources might need to carry fuel for several days' or nights' flight. Also, in order to cross major barriers, a fuel load for several flight stages in a row might be necessary (cf Fransson *et al* 2008). Alerstam & Lindström (1990) found that the majority of passerine migrants carry 20–30% fuel load when departing on migration with no major barriers ahead, but the fuel load increases to 40–70% close to, for example, the Saharan desert. They predicted the optimal fuel load in time-selected migration to be 24%.

Migration strategies differ between as well as within species. Different age classes might have different migration behaviour and time of season might also influence the distance covered in one flight stage. For example, Bensch & Nielsen (1999) found that Sedge Warblers *Acrocephalus schoenobaenus* migrated at a higher speed (average 55 km/d) compared to Reed Warblers *Acrocephalus scirpaceus* (average 39 km/d) during autumn and, in accordance with this, fuel loads (Hall 1996) and average recovery distances from the ringing sites (Bensch & Nielsen 1999) differ between Reed and Sedge Warblers in Sweden during autumn.

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Furthermore, the fuel loads of Sedge Warblers increase with date (Hall 1996).

The aim of the present study was to investigate how far long-distance migrating passerines fly during one migratory flight stage and, with no major barriers ahead, whether or not they perform more than one flight stage consecutively.

## METHODS

### Data collection

In this study, recoveries of 27 passerine species ringed in Sweden and recovered up to, and including, the year 2007 were analysed (Table 1). All species included are long-distance migrants with the main wintering area, for the populations concerned, in Africa south of the Sahara. Species with fewer than 10 recoveries were excluded. Most of the species included are nocturnal migrants, but a few also perform migratory flights during daytime.

Short-term recoveries, for example recoveries the day after the birds were ringed, will include less stopover time compared to recoveries with a longer time interval between ringing and recovery. For this reason, the focus of this study was short-term recoveries. The analyses were based on recoveries with the following three criteria, 1) recovered within seven days from ringing, 2) recovered at least 50 km from the ringing site in the expected seasonal direction (south or north of an E-W axis in autumn and spring, respectively) and 3) reported without any indication of finding date not being exact. This follows Hildén & Saurola (1982) who considered all migration distances below 50 km as local movements. The data included birds ringed in breeding areas as well as on migration, and autumn and spring recoveries were pooled unless stated otherwise.

### Statistical analysis

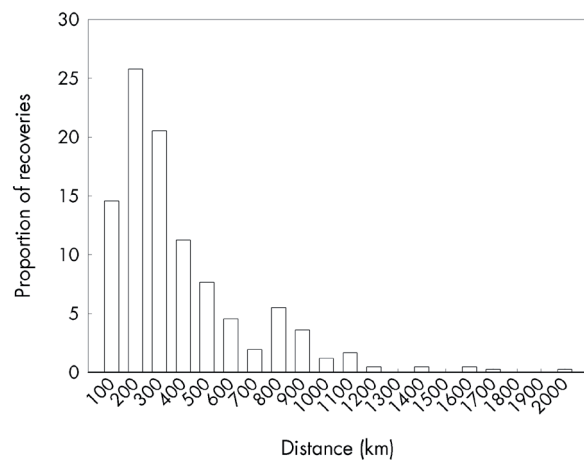
All statistical analyses were performed with STATISTICA 8.0 (Statsoft Inc., Tulsa, OK). Differences between observed and expected distributions were tested by Chi-square; non-parametric tests (Spearman rank correlation) were used to find out if speed estimates were affected by time of season, and differences between speed estimates were tested using Mann-Whitney U-tests.

## RESULTS

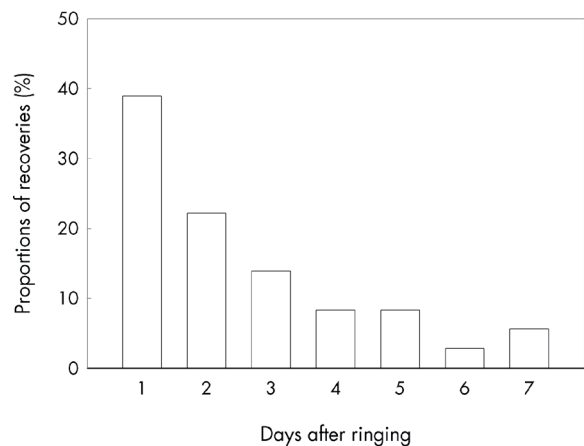
There were in total 11,926 recoveries of the 27 species investigated (Table 1). Of these, 419 recoveries of 21 species fulfilled criteria for inclusion in the analysis. The distances covered by the recovered birds varied between 50 and 1,978 km, with a median distance of 254 km (Fig 1). The largest

number of recoveries were between 100 and 300 km from the ringing sites. Most of the recoveries (81%) were from autumn migration. The migration speed was higher in spring than in autumn (median 76.5 km/d and 56.0 km/d, respectively,  $Z=2.66$ ,  $P < 0.01$ ). Many of the recoveries were aged as juveniles or adults at the time of ringing. In autumn, adult birds had a higher migration speed than juveniles ( $Z = 2.94$ ,  $P = 0.01$ ) but this was not the case for birds ringed and recovered during spring migration ( $Z = 0.56$ ,  $P = 0.60$ ).

In total, 36 recoveries representing eleven species (8.6%,  $n = 419$ ) indicated a migration speed of at least 200 km/d. The proportion of such high-speed recoveries in relation to all recoveries decreased as follows: one day after ringing 38.9% of the recoveries indicated a migration speed of at least 200 km/d; two days after ringing these recoveries were 22.2% of all two-day-recoveries; three days after ringing they were 13.9% of all three-day-recoveries and so on (Fig 2).



**Figure 1.** The distribution of distances from ringing sites for recoveries reported within seven days after ringing, in bands of 100 km. Recoveries within 50 km are excluded.



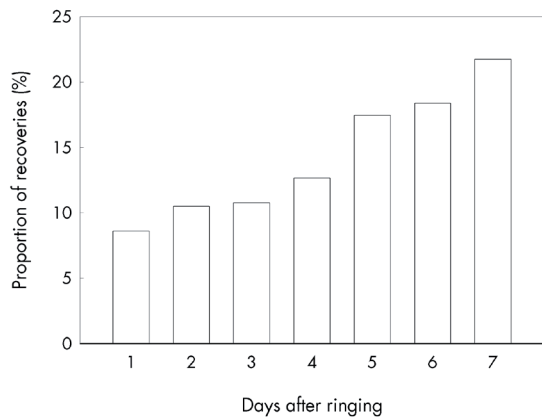
**Figure 2.** The proportion, for each day after ringing, of recoveries indicating a migration speed of at least 200 km/d.

**Table 1.** Data used for analysis. Species included in the study, total number of recoveries of each species during the period 1911–2007 (Recoveries), number of selected recoveries included in the study (for selection criteria see Methods), number of selected recoveries within 24 hours from ringing (Next day), number of selected recoveries at least 200 km from the ringing site within 24 hours from ringing (>200 km, next day), total number of selected recoveries indicating a migration speed of at least 200 km/d (>200 km/d, <8 days), and total number of selected recoveries indicating a migration speed of at least 300 km/d (>300 km/d, <8 days).

Species	Recoveries	Selected recoveries	Next day	> 200 km (next day)	> 200 km/d (<8 days)	> 300 km/d (<8 days)
Sand Martin <i>Riparia riparia</i>	624	1				
Swallow <i>Hirundo rustica</i>	375	3				
House Martin <i>Delichon urbicum</i>	180	0				
Tree Pipit <i>Anthus trivialis</i>	94	1	1	1	1	
Yellow Wagtail <i>Motacilla flava</i>	375	20	2			
Thrush Nightingale <i>Luscinia luscinia</i>	79	1				
Redstart <i>Phoenicurus phoenicurus</i>	467	19	1		3	
Whinchat <i>Saxicola rubetra</i>	88	0				
Wheatear <i>Oenanthe oenanthe</i>	107	0				
Grasshopper Warbler <i>Locustella naevia</i>	15	2	1			
Sedge Warbler <i>Acrocephalus schoenobaenus</i>	798	73	4	3	7	5
Marsh Warbler <i>A. palustris</i>	88	7				
Reed Warbler <i>A. scirpaceus</i>	2,888	153	5	1	8	1
Great Reed Warbler <i>A. arundinaceus</i>	130	1			1	
Icterine Warbler <i>Hippolais icterina</i>	60	2				
Blackcap <i>S. atricapilla</i>	301	9				
Garden Warbler <i>S. borin</i>	260	14	3	1	3	1
Barred Warbler <i>Sylvia nisoria</i>	23	0				
Lesser Whitethroat <i>S. curruca</i>	243	14	4	2	3	
Common Whitethroat <i>S. communis</i>	236	4	1			
Wood Warbler <i>Phylloscopus sibilatrix</i>	44	0				
Willow Warbler <i>P. trochilus</i>	1,344	73	8	2	4	1
Spotted Flycatcher <i>Muscicapa striata</i>	178	5	1			
Collared Flycatcher <i>Ficedula albicollis</i>	401	0				
Pied Flycatcher <i>F. hypoleuca</i>	2,282	7	2	2	2	1
Red-backed Shrike <i>Lanius collurio</i>	228	9	3	2	3	
Ortolan Bunting <i>Emberiza hortulana</i>	18	1			1	1
	<b>11,926</b>	<b>419</b>	<b>36</b>	<b>14</b>	<b>36</b>	<b>10</b>

Of the 419 recoveries, 36 (8.6%) were recovered within 24 hours from ringing. This is much less than would be expected by chance (419 recoveries in seven days equals 60 recoveries a day). A closer look at the distribution of recoveries over the seven days revealed that fewer birds than expected by chance were reported during the first four days after ringing whereas this proportion was higher than expected by chance during days 5–7 (Fig 3, Chi-square 42.1, df 6,  $P < 0.001$ ). The 36 recoveries within 24 hours from ringing represent thirteen species with 1–8 recoveries each (median two recoveries). Fourteen of these recoveries (40.0%) were reported at least 200 km from the ringing site and four of them (14.8%) were found more than 300 km from the ringing site during

the day after ringing. In total, there were 10 recoveries of six species (2.4%) where the average migration speed exceeded 300 km/d (Table 1). Five of these were Sedge Warblers and one recovery each of Garden Warbler *Sylvia borin*, Reed Warbler, Willow Warbler *Phylloscopus trochilus*, Pied Flycatcher *Ficedula hypoleuca* and Ortolan Bunting *Emberiza hortulana*. A few birds had covered impressive distances over 6–7 days, eg an Ortolan Bunting ringed on southernmost Gotland and found in southwestern France (1,978 km) six days later, a Garden Warbler ringed in central Sweden and found in Italy (1,562 km) seven days later and a Sedge Warbler ringed in central Sweden and controlled by ringers in Slovenia (1,524 km) seven days later (Fig 4).



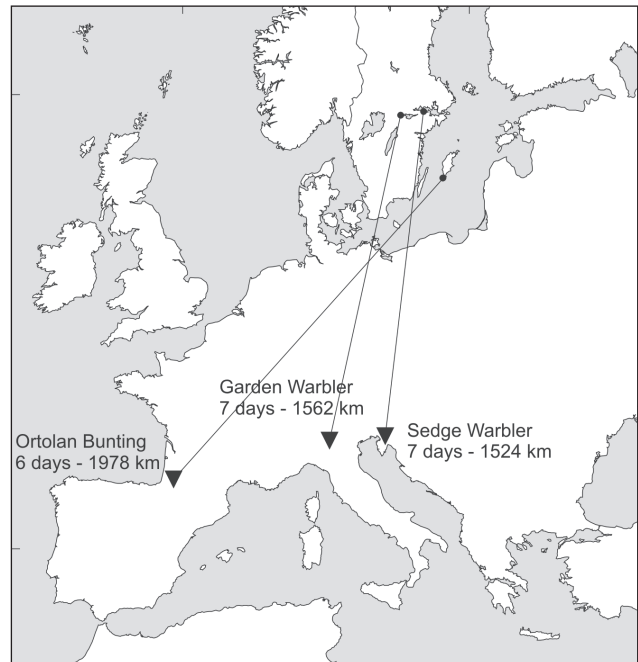
**Figure 3.** The proportion of the selected recoveries ( $n = 419$ ) reported each day after ringing. The average proportion of recoveries per day is 14.3% (60 recoveries).

For all recoveries within seven days, there was no correlation between migration speed and date during autumn ( $r_s = -0.018$ ,  $n = 339$ ,  $P = 0.75$ ), but a significant positive correlation with date in spring ( $r_s = 0.28$ ,  $n = 80$ ,  $P = 0.013$ ). With respect to recoveries obtained within 24 hours of ringing (all species combined), there was no correlation between distance covered in one flight stage and date during either autumn ( $r_s = 0.077$ ,  $n = 20$ ,  $P = 0.74$ ) or spring ( $r_s = 0.012$ ,  $n = 16$ ,  $P = 0.96$ ).

A few species had enough recoveries within seven days from ringing for separate analyses of migration speed. Of these, juvenile Willow Warblers increased migration speed with the progress of the autumn ( $r_s = 0.34$ ,  $n = 34$ ,  $P = 0.049$ ), but this was not the case for juvenile Sedge Warblers ( $r_s = 0.12$ ,  $n = 66$ ,  $P = 0.33$ ) or juvenile Reed Warblers ( $r_s = -0.02$ ,  $n = 128$ ,  $P = 0.79$ ).

## DISCUSSION

The distances covered by the selected recoveries show a large variation with a median distance of 254 km and 36 recoveries of 11 species indicated a migration speed of at least 200 km/d. This suggests that a migration distance of more than 200 km during one flight stage is not unusual. The proportion of recoveries indicating a migration speed of at least 200 km/d decreased for each day after ringing, which is to be expected as more stopover time is included in the speed estimates for each day in the interval between ringing and recovery while on migration. Migration speed was found to be higher in spring than in autumn, based on the selected recoveries, and this has also been shown in earlier studies (Fransson 1986, 1995). Speed of migration has been shown to be higher for individuals ringed later in the season (Fransson 1995, Bensch & Nielsen 1999) and this was also the case for juvenile Willow Warblers in the present study. Sedge Warblers and Reed Warblers,



**Figure 4.** Examples of some fast movements over longer distances of birds ringed in Sweden.

on the other hand, did not show any correlation between date of ringing and migration speed. When all species were analysed together no correlation between time of season and speed was found in autumn while speed increased during spring. Higher speed estimates in spring, as well as an increased speed in late birds, might be a result of the importance of an early arrival at the breeding sites. Adult birds migrated at a higher speed compared to juvenile birds in autumn but no such difference could be found in spring.

The selected recoveries were distributed unequally over the seven days after ringing, with fewer recoveries during the first four days and more recoveries than expected by chance on days five to seven. This pattern might be explained by the fact that many of the recovered birds were ringed at places where they had just landed after completing a migratory flight (*cf* Zehnder & Karlsson 2001). Birds ringed the day after a migratory flight might often need to stay and refuel for some days before continuing on migration and the pattern shown indicates that a refuelling time of more than four days is common. In comparison, at the southern end of the Swedish island Öland, median stopover times varied from two to seven days for six long-distance migrating passerines, and four of the six species had median stopover times of 4–5 days (Åkesson *et al* 1995). Schaub & Jenni (2001), on the other hand, estimated stopover times by statistical modelling to be 7.7 days in Garden Warblers, 9.1 days in Sedge Warblers and 9.5 days in Reed Warblers migrating within Europe. If

these estimates are correct, and stopover time is 8–9 days, only every ninth or 10th bird trapped at a stopover site is close to performing a migratory flight. Also, if stopover time is eight days and birds only perform one flight stage in a row, a bird will after a flight stage be found the next day at the same distance from the ringing site as a bird that is recovered after nine days. In order to reach their wintering quarters on time, birds staying for 8–9 days on stopover sites have to migrate at least two nights in a row before refuelling.

A stopover site might not necessarily be as good as it looks from the sky, since it could be crowded with conspecifics, food availability might be lower than last time (for an experienced bird) or predation risk might be high (Fransson & Weber 1997). If a bird lands in a less-than-optimal stopover area, for example because of daybreak or bad weather, it has to decide whether to stay or to move to a better area. In this case shorter movements the following night might be the best strategy, continuing in the migratory direction and hoping for a better stopover site later on (cf Moore & Aborn 1996). This is supported by capture–recapture data from stopover sites where it was shown that individuals that lost fuel stores departed earlier than individuals that accumulated fuel at medium rates (Schaub *et al* 2008). In accordance with this, Gwinner *et al* (1988) showed that migratory restlessness increased when Garden Warblers experienced food deprivation and decreased when given unlimited access to food. Some of the observed shorter movements in this study might be explained by such behaviour.

It is unclear what length of time a bird on migration actually spends on the wing before resting, *ie* how many hours during the night do nocturnal migrants spend flying, and vice versa for diurnal migrants. Ellegren (1993) estimated the average flight time to be 3.3 hours a day for diurnal migrants and that the period spent flying during the night by nocturnal migrants was shorter than the length of the dark period (range 1–15 hours). Åkesson & Hedenström (2000) estimated the mean departure time for passerines from Öland, SE Sweden, to be one hour after sunset and Reed Warblers leaving Russia on autumn migration started night movements on average in the fourth hour of the night (Muhkin *et al* 2005). Zehnder *et al* (2001) found a pronounced peak of migratory intensity during the first half of the night, indicating that birds begin to land after only 3–6 hours of flight. Reed Warblers on spring migration were estimated to fly for 4–6 hours and based on fuel loads of birds landing it was assumed that many of them fly several nights in a row (Bolshakov *et al* 2003). Schaub & Jenni (2001), on the other hand, used a 10-hour night for their mathematical modelling estimations and Liechti & Schmaljohann (2007) found that migration of songbirds

over the Saharan desert continued with stable numbers from sunset to sunrise.

Bloch & Bruderer (1982) estimated air speed (the speed produced by flapping wings) from radar observations to be 12.6 m/s (= 45 km/h) in passerines. If migration time in one night is eight hours, a passerine bird would be able to migrate 360 km/night without any wind assistance. In the recoveries used for this analysis, there were three recoveries of Sedge Warblers with distances of this magnitude: 345 km, 351 km and 381 km from the ringing site on the day after ringing. There were also two recoveries of Sedge Warblers three days after ringing, indicating a similar level of migration speed. One bird was recovered 1,191 km from the ringing site, corresponding to 397 km per night, and the other was recovered 974 km from the ringing site three days later, indicating a migration speed of 325 km per night. It is possible that these two birds could have migrated in extremely good tail wind conditions and covered about 1,000 km during one night flight, but this is highly unlikely (cf Alerstam 2003). It is more likely that they had flown for several nights in a row, with daytime rests in between, before refuelling at stopover sites. The same is also true for some other birds that moved long distances within seven days from ringing. The Ortolan Bunting is a species that sometimes migrates in daytime as well, but even if this were the case with the bird moving from Sweden to France during six days, the average speed was 329 km/d.

Since stopover is the most time-consuming part of bird migration it would save time, although not energy, to migrate several nights or days in a row instead of resting several days after each flight. The disadvantage of flying several days or nights in a row is the need for a larger amount of fuel, which makes the flight more costly. Predation risk will also increase with a higher body mass. Flight-range estimates of *Sylvia* warblers on southern Gotland, in the Baltic, showed that the 25% fattest fraction of the Lesser Whitethroats and Whitethroats had enough fuel to fly for two nights, Blackcaps for four nights and Garden Warblers for five nights in a row (Ellegren & Fransson 1992). These estimates are based on the assumption that all fuel is available for flight, but since it might take some time to start efficient foraging at a new location it might be wise not to use all of the fat reserves before landing at a stopover site (cf Alerstam & Lindström 1990).

In conclusion, short-term ringing recoveries show that the distances covered by migratory birds during a flight stage can vary considerably, but long-distance passerine migrants may regularly fly several flight stages in a row, with short rests in between, before refuelling, even if there are no major barriers ahead.

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