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The migration system of Common Snipe *Gallinago gallinago* on autumn passage through Central Europe

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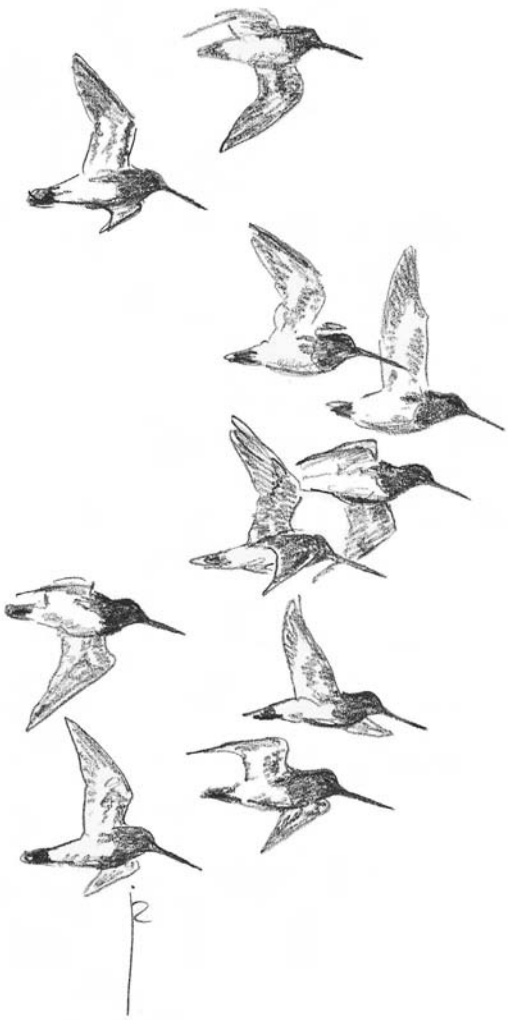

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The Common Snipe *Gallinago gallinago* migrates in large numbers through central Europe towards its wintering grounds in western Europe. Over the past 20 years more than 12 000 Common Snipes were ringed at seven ringing stations in Poland during their autumn migration. Birds migrating along the Baltic coast tended to spend the winter in more northern areas than those that used southern Poland as stopover sites during migration. This pattern supports the hypothesis of a parallel autumn migration exhibited by Common Snipe. Additionally, snipes passing through Poland at the beginning of the autumn migration (originating from near breeding areas) overwintered further north than later migrants (known to originate from more northern areas), which is consistent with a leap-frog migration pattern. Our results suggest that the migration pattern of the Common Snipe is more complex than previously thought, because these birds use a combination of two different non-exclusive migratory patterns.

Key words: Common Snipe, *Gallinago gallinago*, direction of migration, wintering grounds, segregation of populations, migration pattern

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The Common Snipe *Gallinago gallinago*, contrary to its English name, is a rare breeding wader in Europe (Kirby & Delany 2009). The situation changes during migration when huge numbers of birds from the more eastern breeding areas pass through central Europe towards their wintering grounds in the western part of the continent. The snipe is also a popular game bird in Europe with an annual hunting bag of more than one million individuals (Devort 1997). Thus, the ring recovery rate of this species is high, though variable among countries (Dhont & van Hecke 1977, Fog 1978, Kålås 1980, Roos 1984, Pörner 1987, Kharitonov 1998, Švažas *et al.* 2001, Meissner 2002). In West Europe, Common Snipes are hunted in autumn and winter (Schies 1997 in Rouxel 2000). Autumn migration routes and the overwinter localities are therefore relatively well-known, though most studies are restricted to the distribution of recoveries without analysing the migratory pattern at the scale of the continent. The distribution of Common Snipe's ringing recoveries has been published for Central Europe (Glutz von Blotzheim *et al.* 1977), Denmark (Fog 1978), Fennoscandia (Kålås

1980, Bakken *et al.* 2003), Britain and Ireland (Wernham *et al.* 2002), the former USSR (Baumanis 1985, Kharitonov 1998), and Poland (Meissner 2002, for the Gulf of Gdańsk).

Kharitonov (1998) and Rouxel (2000) noted that different populations of the Common Snipe occupied different wintering areas, though without clear-cut borders. However, the migratory pattern of the Common Snipe proposed in both studies is speculative, and is not based on a statistical analysis of the distribution of recoveries. Geographical differences in migratory routes and wintering areas of distinct populations are observed both in waders and non-waders (Hale 1980, Berthold *et al.* 2003). For example, Dunlins *Calidris alpina* from western Russia spend the winter mainly in north-western Europe, but birds from central Siberia migrate to north Africa (Lundberg & Alerstam 1986, Wennerberg 2001). Turnstones *Arenaria interpres* from Greenland winter in western Europe, whereas birds from Siberia migrate to southern Africa (Summers *et al.* 1989). The inter-population variation in the migration flyways of different species is the basis for the classification of migratory systems in birds (Newton 2008). Within this classification, a 'parallel migratory system' describes a situation in which the migratory route of a northerly breeding population runs parallel to its southern equivalent. The term 'leap-frog migration' refers to birds from more northern breeding grounds to use more southern wintering areas. Such migratory patterns operate at a large geographical scale, and can be detected by comparing populations from different countries or parts of a continent.

This paper aims to show an inter-population difference in migratory direction and wintering grounds for the Common Snipes passing through Poland during autumn migration.

METHODS

Study area

Common Snipes were ringed during the autumn migration (July–September) in 1983–2006 at seven ringing sites in Poland (Fig. 1), where more than 12 500 Common Snipes were caught. Most of the birds were caught in walk-in traps, and occasionally by mist nets (Włodarczyk *et al.* 2005, Meissner *et al.* 2006). We divided the ringing sites into a southern and northern group (Fig. 1). The first group consisted of two dam reservoirs, Jeziorsko (51°40'N, 18°40'E) and Turawa (50°43'N, 18°08'E), and one river floodplain , Słońsk (52°34'N, 14°43'E). The northern group included

Figure 1. Ringing sites of the Common Snipe in Poland and the delineation in northern and southern sites.

Jastarnia (54°42'N, 18°40'E) and the Reda river mouth (54°39'N, 18°30'E) (both at Puck Bay), Lisewo Malborskie (54°06'N, 18°49'E) (in the lower Vistula valley), and Kolonia Nisko (54°04'N, 21°03'E).

Data analysis

Following common practice, we used wing length as an indicator of the birds' body size (e.g. Hedenström 2004). Bill length was used as a proxy for sex although this measure does not allow a very accurate distinction (McCloskey & Thompson 2000). To restrict variation within samples by sex and population, biometrical analyses were performed only on adult snipes (O'Connor 1997).

A direct ringing recovery was defined as a recovery within the same autumn or winter after ringing. As in other studies (Kålås 1980, Baumanis 1985), birds recorded between the beginning of December and the end of February where considered to be winter recoveries. Analyses of migration direction and distance were confined to direct recoveries.

Common Snipes ringed in southern and central Poland did not differ in the location of the wintering grounds (Wilks test: $F_{2,171} = 2.08$, $P = 0.086$), and did not differ in the mean direction of migration (Watson & Williams test: $F_{2,171} = 1.66$, $P > 0.1$). Therefore, data from all southern sites were combined. Similarly, the data from the northerly sites were treated jointly, although we were not able to test any differences in migration behaviour due to small sample sizes at each site. Nevertheless, since all the sites were located close to each other and at similar latitudes, we believe these sites likely hosted snipes from the same populations during autumn migration. This division was also supported by the birds' movements between the ringing sites in the southern group, and because no birds from one group were recovered in the other group.

Snipes ringed before the median ringing date (12 August at Jeziorsko reservoir) were considered to be early migrants, those ringed after the median date were treated as late migrants. The direction of migration was calculated by a loxodromic formula (Imboden & Imboden 1972) from the geographical coordinates. North was referred to as 0°. We checked the differences in the direction of migration using the Watson–Williams test. Circular statistical analyses were performed using Oriana 2.0 and followed Batschelet (1981) to arrive at mean angles of migratory direction and standard deviations around these means. Mean locations of recoveries were calculated as the means from the coordinates of particular points, which followed other studies (Bairlein 2001, Remisiewicz 2002). Differences between the mean coordinates of two groups of points were tested with the Hotelling test, and when more groups were compared we used the Wilks test. Statistical methods for linear variables were based on Zar (1996) and the analyses were performed using STATISTICA 6.0 PL (StatSoft 2003).

RESULTS

Ringing recoveries

In total, 327 Common Snipes were recovered by the spring of 2008 (Table 1, Fig. 2), which gave a recovery rate of 2.5%. Most of the recoveries (71%) came from France, which reflects the high hunting pressure in that country. The proportion of recoveries from France did not differ between snipes ringed in the northern and southern ringing locations (60.9% vs. 73.6%; Chi-square test with Yates' correction: $\chi^2 = 3.71$, $df = 1$, $P = 0.054$), hence the results from the northern and southern locations were similarly affected by the preponderance of French recoveries. As the direction of migration may change over the course of the season

Table 1. Numbers of recoveries obtained for Common Snipes ringed at different sites in Poland. Direct recoveries were reported within the autumn/winter following ringing. Indirect recoveries were reported later in time.

Site	Direct recoveries	Indirect recoveries	Total
Southern sites			
Jeziorsko	103	54	157
Słońsk	49	26	75
Turawa	19	9	28
Northern sites			
Reda Mouth	15	13	28
Jastarnia	17	10	27
Kolonia Nisko	4	3	7
Lisewo Malborskie	2	3	5

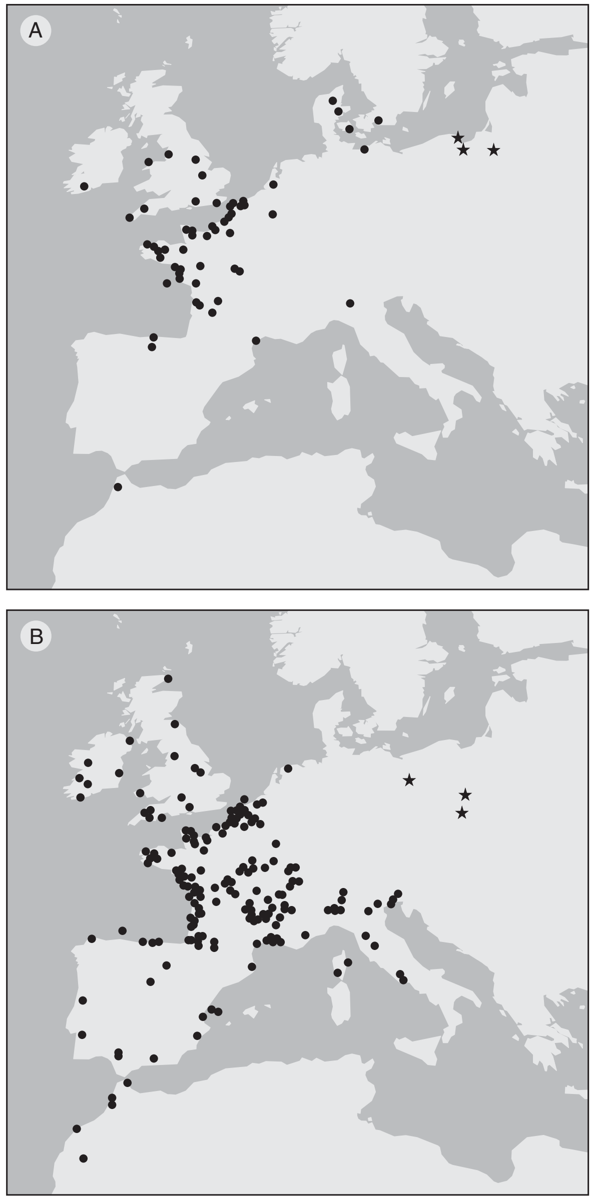

Figure 2. Recoveries during autumn and winter of Common Snipes ringed at northern (A) and southern (B) ringing sites in Poland (stars).

(Meltofte 1996), differences in timing of the migration and ringing activities could have affected our results. However, our observations did not suffer such a bias as the median dates of passage of Common Snipes passing through the northern and the southern sites proved to be similar (Mann–Whitney U-test, $U = 8315.5$, $n_1 = 258$, $n_2 = 66$, $P = 0.77$).

Direction and distance of migration

Common Snipes ringed in southern Poland migrated in a significantly more southerly direction (mean migration angle: 243°, SD 17.15, $n = 71$) than those from northern Poland (mean migration angle: 249°, SD 14.26, $n = 38$; Watson–Williams test: $F_{1,209} = 11.22$, $P < 0.001$). Nonetheless, the birds from both groups covered similar distances to reach their wintering grounds (1370 km, SD 368.7, $n = 60$, vs. 1388 km, SD 302.0, $n = 16$, respectively; *t*-test: $t_{74} = 0.19$, $P = 0.85$).

Data obtained from the southern ringing sites showed that the ringing date correlated significantly with the bird's direction of migration ($r = -0.257$, n = 169, $P < 0.001$). In general, the later the individuals were caught, the more southerly was their direction of migration. For example, at Jeziorsko reservoir, which provided the highest number of direct recoveries, late migrants chose a migration direction 7 degrees more to the south than early migrants (238.5°, SD 14.5, $n = 51$ vs. 246.3°, SD 18.7, $n = 52$; Watson–Williams test: $F_{1,103} = 5.90$, $P < 0.025$, Fig. 3).

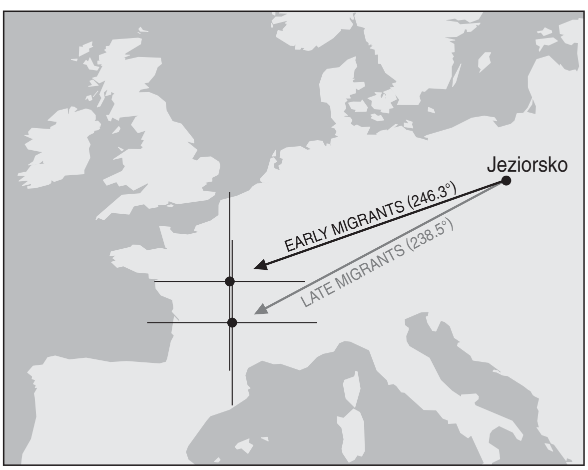

Figure 3. Directions of migration of Common Snipes passing through Jeziorsko reservoir during early (black arrow) and late (grey arrow) autumn. Destination points represent the mean locations of direct recoveries for each group of migrants, respectively, with standard deviations.

Biometrical analyses revealed a positive correlation of the wing length of adults with date of ringing at Jeziorsko reservoir ($r = 0.226$, $n = 382$, $P < 0.001$). The later migrants showed longer wings than those ringed earlier in the season. No such relationship was found for bill length ($r = 0.001$, $n = 382$, $P = 0.98$), suggesting that males and females did not differ in their timing of migration.

Recoveries to the east of Poland, which would indicate the breeding origin of the Common Snipes, were obtained mainly from birds ringed at the southern ringing sites. The mean location of these recoveries was 54°35'N, 33°13'E and the mean migration direction was 258° (SD = 14.22, $n = 7$). This indicated a migration along the same latitude from the breeding grounds to central and southern Poland, and consequently the eastern and north-eastern origin of birds caught in this part of the country. The exact location of the breeding grounds of these snipes remains unknown, because most of the recoveries come from the autumn. The only recovery indicating the breeding origin of snipes ringed in northern Poland suggests that they come from far further north, as the angle of the migration of the recovered bird was 230° (Fig. 4).

Wintering grounds

The wintering grounds differed between snipes ringed in northern and southern Poland (Hotelling test: $F_{2,116} = 5.36$, $P = 0.006$, Fig. 5). Though Common Snipes ringed in northern Poland spent the winter at significantly higher latitudes than birds ringed at the southern sites (*t*-test: $t_{117} = 3.19$, $P = 0.002$), the mean longitude of both groups' wintering areas did not differ (*t*-test: $t_{117} = 0.83$, $P = 0.41$). The difference in latitude for overwintering snipes follows from a more detailed analysis of distribution in France, as a main wintering ground for snipes passing through Poland, as well. In France, the 48°N line of latitude separates the coastal areas along the English Channel from the central and Mediterranean regions of the country. A significantly greater proportion of the snipes passing through northern Poland wintered at latitudes higher than 48°N in comparison with those ringed at the southern sites (68% vs. 35%, Chi-square test with Yates' correction: $\chi^2 = 8.57$, $df = 1$, $P = 0.003$). Moreover, the difference between northern and southern ringing locations in the proportions of birds recovered in Britain was especially large (Chi-square test with Yates' correction: $\chi^2 = 6.58$, $df = 1$, $P = 0.010$). About one-third of the recoveries of snipes ringed at the northern sites came from Britain, in contrast to only 10% of recoveries of birds ringed at the southern sites in Poland.

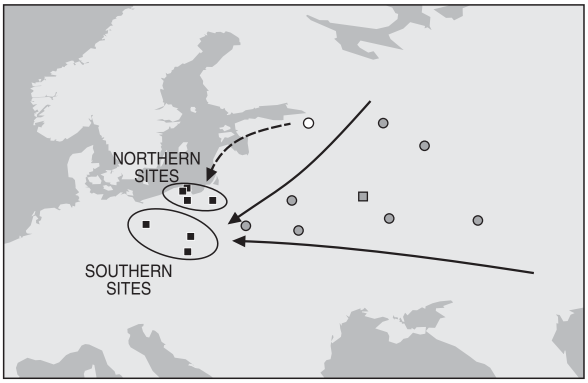

Figure 4. Eastern recoveries of Common Snipe caught at southern (filled circles, area delimited by black arrows) and northern (open circle, dotted arrow) ringing sites. The mean location of the recoveries from the southern sites is marked with a grey square.

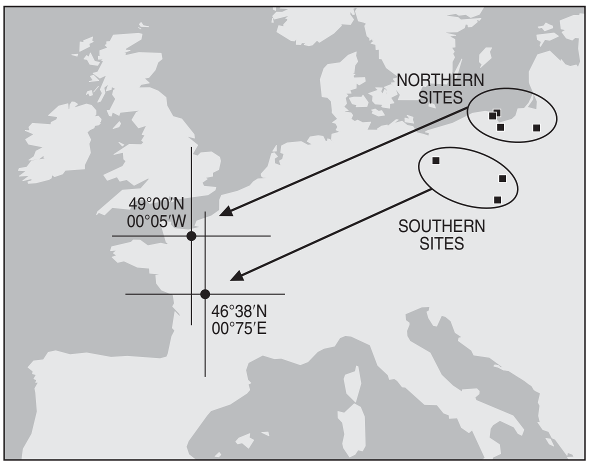

Figure 5. Mean locations of the wintering grounds of Common Snipes passing through northern and southern Poland in autumn, with standard deviations.

DISCUSSION

Our analysis of ringing recoveries showed that birds passing through the northern part of Poland used mainly the coastal migratory route and their wintering areas were situated further north than those of birds migrating through the central part of the country. Birds from Finland and northern Russia probably migrate along the Polish coast, but birds breeding in Belarus and central Russia are thought to migrate over an inland route. This assumption is supported by our ringing recoveries, which showed that snipes migrated due west from their breeding grounds to central and southern Poland. The analysis of ringing recoveries from Russia performed by Kharitonov (1998) revealed a similar pattern. Additionally, there were no ringing recoveries of Common Snipes at southern Polish ringing sites that were ringed at the northern Polish ringing sites, or vice versa, which confirms the existence of two separate corridors for the Common Snipe's autumn migration through Poland. The migratory division of snipes between the northern and southern regions of Poland is similar to the pattern observed in other parts of Europe. Fog (1978) showed that birds from the western part of Denmark spent more often the winter in Britain than birds ringed in eastern Denmark. According to Kålås (1980), this observation reflects the different breeding origins of these groups of birds as some breed in Norway, others in Finland and Sweden. An analysis of recoveries of birds caught in the former USSR (Baumanis 1985) also showed that birds migrating over the Baltic coast were found later in the season mainly in Denmark, The Netherlands and Britain along the Atlantic coast, similar to snipes caught at northern stations in Poland. Individuals ringed in central Russia were more frequently observed inland, especially in Germany and France, which is consistent with our birds ringed in central and southern Poland. Our results support the previous work of Meissner (2002), who showed that Common Snipes passing through northern Poland almost exclusively follow the southern Baltic and the Atlantic coasts on migration. Such a stratification of migratory routes from north to the south is consistent with the pattern described by Devort *et al.* (1986 in Rouxel 2000) and Kharitonov (1998). These authors suggest that breeding populations from Scandinavia and the eastern Baltic region use the Baltic and the North Sea coast during migration and head towards Britain and the Atlantic coast of France. In contrast, Common Snipes breeding in central Russia pass through Poland and Germany to the Atlantic coast of France, and birds breeding in southern Russia and Ukraine pass through former Czechoslovakia and Austria to the Mediterranean coast of France, Italy and former Yugoslavia.

A geographical separation of different populations during migration and wintering has been described for a number of wader species. For example, Purple Sandpipers *Calidris maritima* of the south Norwegian breeding population winter in eastern Britain, Iceland's sedentary population winters locally and birds breeding in Russia winter in northern Norway (Summers *et al.* 2004). Generally speaking, it appears that in species with a parallel migration pattern the populations from the western part of the breeding range winter further to the west than populations that breed further east (and these occupy the eastern part of the wintering areas). This type of migration is common in waders and was described in Golden Plovers *Pluvialis apricaria*, Whimbrels *Numenius phaeopus* and Dunlins *Calidris alpina* (van de Kam *et al.* 2004).

The shift in the migratory direction between early and late migrants at Jeziorsko reservoir suggests a leap-frog type of migration (Salomonsen 1955). A leap-frog migration pattern in Common Snipe has also been suggested by Tuck (1972), Cramp & Simmons (1997) and Rouxel (2000). Unfortunately, our data set lacks direct recoveries from the breeding grounds that could give insight into the origin of individuals ringed in the different periods of migration in Poland. However, we can give two pieces of indirect evidence for the northern origin of late migrants. Firstly, individuals caught at the beginning of autumn probably originate from breeding grounds close to the Polish ringing sites because the Common Snipe follows an energy-minimization strategy during autumn with a low speed of migration (Włodarczyk *et al.* 2007). Breeders from further north-east are expected therefore to need more time to reach Poland and appear later in the autumn. Secondly, we found a gradual increase in body size (wing length) at Jeziorsko reservoir during the autumn passage, which – assuming Bergman's rule applies to Common Snipe populations (Ashton 2002) – indicates the passage of gradually more north-eastern breeding populations through central Poland.

Apart from these explanations, the gradual shift in direction of migration might have been caused by a sex-related phenology of migration. Devort (1997) analysing the sex ratio of adult birds shot in France suggested that males migrated earlier and stayed closer to the breeding grounds than females. However, using bill length as a sex-dependent trait in the Common Snipe (Prater 1977, McCloskey & Thompson 2000), we found no indication at all of a shift in sex ratio. Therefore it seems more plausible to explain the differences in the direction of migration between early and late migrants in terms of a population shift instead of sex-related segregation.

In conclusion, our results suggest that the migration pattern of the Common Snipe is composed of a parallel migration (separating populations along a latitudinal gradient) and leap-frog migration (a different migration for populations along a longitudinal gradient). Both types of migration are not mutually exclusive and might well coexist within one species, as was described in the Dunlin (Wennerberg 2001, Lopes *et al.* 2008).

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SAMENVATTING

De Watersnip *Gallinago gallinago* trekt in groten getale door Midden-Europa op weg naar de overwinteringsgebieden in West-Europa. In de afgelopen 20 jaar werden op zeven plekken in Polen meer dan 12.000 Watersnippen tijdens de herfsttrek geringd. Op grond van de ringvondsten bleken de snippen die langs de Oostzeekust trokken, noordelijker te overwinteren dan snippen die door Midden- en Zuid-Polen passeerden. Dit is een aanwijzing voor een parallelle herfsttrek bij deze soort. Daarnaast overwinterden snippen die vroeg in de herfst werden gevangen (afkomstig uit nabijgelegen broedgebieden) noordelijker dan snippen die later in de tijd waren geringd (afkomstig uit oostelijker gebieden). Daarmee laat dit onderzoek zien dat het trekpatroon van de Watersnip waarschijnlijk ingewikkelder is dan eerder werd gedacht. (DH)

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