

## Different migration strategies used by two inland wader species during autumn migration, case of Wood Sandpiper *Tringa glareola* and Common Snipe *Gallinago gallinago*

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Waders generally follow two alternative strategies. The “B-strategy” or “energy minimization” strategy is to initiate migration late in the season, start moulting at the breeding grounds and migrate slowly in small steps, whereas the “S-strategy” or “time minimization” is to migrate immediately after the end of the breeding period and moult on the wintering grounds after a migration with only a few stopover sites. We studied Wood Sandpipers *Tringa glareola* and Common Snipes *Gallinago gallinago* at the Polish Jeziorsko reservoir. Adult and juvenile Wood Sandpipers migrate during different periods, and showed no signs of moult. In contrast, both age groups of Common Snipe migrate during the same period, and up to 30% of ringed adult Common Snipes had started their post-breeding moult at the reservoir. Wood Sandpipers stayed 4–5 days at the reservoir, where they fattened at a rate of 1.15 g/day (which was positively correlated with their length of stay,  $r = 0.21$ ), and left with 21% of fat (% of LBM), allowing them to cover distances exceeding 2,500 km (which enables them to reach the coast of the Mediterranean Sea). In contrast, Common Snipes stayed 11 days, fattening 0.3 g/day, and left the reservoir independently of their fat reserve. Common Snipes stored a significantly smaller fat reserve than Wood Sandpipers, and their reserve was predicted to allow maximally 1,500 km of constant flight. Our findings support the hypothesis that, under common feeding conditions at Jeziorsko reservoir, Common Snipes behave according to the energy minimization strategy whereas Wood Sandpipers use a time minimization strategy.



## 1. Introduction

Waders belong to birds performing annual migration between breeding and wintering grounds (del Hoyo *et al.* 1996). Distances travelled can differ between species, age classes and sexes (Meissner 2001). Some Palearctic species such as Red Knot *Calidris canutus*, Ruff *Philomachus pugnax* or Great Snipe *Gallinago media* travel up to a few thousand kilometres between their breeding grounds, located in Siberia, and wintering grounds in central or southern Africa (Snow & Perrins 1998). Other species such as Lapwing *Vanellus vanellus* or Common Snipe *Gallinago gallinago* may fly only a few hundred kilometres during migration (Cramp & Simmons 1986). Moreover, their breeding populations in western Europe don't migrate, because their wintering grounds overlap their breeding ranges. Such diversity observed in wader migration has created a high level of interest and a number of extensive studies.

Distance travelled during migration, location of breeding and wintering grounds, moult period and finally migration strategy were used by Alerstam and Högstedt (1982) to divide birds into two main types: S- and B-species. Population size of the first group is limited by a shortage of favourable conditions or resources at breeding grounds. S-species try to minimize time spent at breeding areas due to strong intraspecific competition, and travel fast to wintering grounds in order to stay there as long as possible. On the contrary, B-species (from "breeding resources") face the most intense intraspecific competition at wintering grounds. As a result, such species postpone migration, slowly travel short distances and stay within wintering grounds for a short period.

The relevance of such division is supported by different migration strategies performed by S- and B-species. Birds which encounter surplus resources at breeding grounds (B-species) migrate in small steps, don't accumulate large fat reserves and use numerous stopover sites. In other words, B-species minimize total energy costs of migration (Alerstam & Lindström 1990). Lapwing, Woodcock *Scolopax rusticola* and Golden Plover *Pluvialis apricaria* are species that perform such a migration strategy (Meissner 2001, van de Kam *et al.* 2004). On the other hand, waders that benefit from surplus resources at "survival grounds" (S-spe-

cies) are time-selected migrants. This strategy is manifested by high speed migration and low number of refuelling sites where birds try to maximize their fuel load necessary for relatively long constant flight (Alerstam & Lindström 1990). Red Knot and Bar-tailed Godwit *Limosa lapponica* are the most well known examples of species that migrate according to these assumptions. Representatives of the same species might differ in the migration strategy performed and can adjust it according to conditions met during migration (Alerstam & Hedenström 1998, Meissner 2001, Helseth *et al.* 2005). In general, these strategies also differ in life histories, including the time and length of moult and the phenology of migration (Alerstam & Högstedt 1982).

Wood Sandpiper *Tringa glareola* and Common Snipe belong to waders that migrate in large numbers across central Europe (Glutz von Blotzheim *et al.* 1977, Cramp & Simmons 1986). They use inland water bodies as resting and refuelling sites, however, both species are treated as representatives of two different life strategies. Common Snipe spends winter in western Europe close to its breeding grounds and migrates slowly so it was classified as a B-species (Melfo 1996). Having a short distance to cover during migration, using even small wetlands as refuelling sites, the Common Snipe seems to be predisposed to use an energy minimization strategy.

On the contrary, Wood Sandpiper, which winters in central and southern Africa, is suggested to be a representative of S-species (Melfo 1996, Meissner 1997a). This wader can use both types of migration strategy depending on the amount of food at refuelling sites (Meissner 1997a, Wichmann *et al.* 2004). Despite the proposed classifications of both species, only the Wood Sandpiper migration strategy has been subjected to thorough examination (Meissner 1997a, Wichmann *et al.* 2004, Remisiewicz & Wennerberg 2006). Papers concerning Common Snipe migration are focused mainly on biometric data and migration phenology (OAG Münster 1975, Meissner 2003).

Moreover, there are no studies analysing features of migration for both species within the same stopover site. In this paper, we analyse migration strategy in connection with the life cycle of Wood Sandpipers and Common Snipes using the same

stopover site and meeting the same feeding conditions during their autumn migration.

## 2. Material and methods

### 2.1. Study site and methods

The study was carried out at Jeziorsko reservoir (51.40° N, 18.40° E), central Poland. Due to regular changes of water level the place creates excellent feeding conditions for waders, especially during their autumn migration (Włodarczyk *et al.* 2005). Ringing of waders was performed at the reservoir annually since 1989. However, proper data was precisely recorded only between 1997–2005. Birds were caught mainly in walk-in traps and occasionally in mist-nets. The time of fieldwork was variable between years. Usually, the data was collected from the beginning of July till the second half of September, with the extreme dates of 25 June 2005 for the beginning and 24 September 2004 for the end of ringing activity. Although this covered the whole Wood Sandpiper autumn migration through central Poland (Tomiałojć & Stawarczyk 2003), it wasn't long enough to investigate Common Snipe migration through the study area in the late autumn. Nevertheless, the fieldwork comprised the main migration waves of Snipes, which appear at Jeziorsko at the turn of August and September (Janiszewski *et al.* 1998). The number of Snipes emerging at the site later in October are comparatively insignificant, thus the data obtained seem to be sufficient for the migration analyses.

There were 3,935 Common Snipes and 4,806 Wood Sandpipers ringed in the seasons 1997–2005. The total numbers of birds caught more than once during one season (retrappings) were 129 and 224, respectively, for each species. All birds were measured and weighed. Measurements taken with 0.1 mm accuracy included total head, tarsus, bill and nalospi lengths. Furthermore, wing in its maximum chord was measured to the nearest 1 mm. All measuring procedures were conducted according to standards described by Busse (2000). The fat loads of each bird were assessed in the furculum and under the wing according to the fat score scale used for waders (Busse 2000). In addition, birds banded in 2004–2005 were carefully

examined in order to specify their moult stage. To this end, each flight-feather (primaries, secondaries, tertials) and rectrice was given a number in the 5-score BTO scale (Ginn & Melville 1983). If possible, moult stages of primary-, greater- and tertial-coverts, alula feathers and carpal-covert were marked analogously. Lesser- and median-coverts were divided into three categories, old, growing and new, and the percentage of each category was noted. The procedure was conducted using special moult-cards.

The species differed significantly in their mean weights (Wood Sandpiper: = 66.3 ± 10.0 (SD), n = 4805; Common Snipe: = 102.0 ± 10.1 (SD), n = 3935). To avoid any influence of such a difference in the comparison, the values of mass changes were converted into percent of the lean body mass (LBM) gained per day. To estimate LBM of the species, the mean weights of birds with fat loads assessed at zero points were calculated. The values were 97.6 g for Common Snipe (n = 757) and 54.2 g for Wood Sandpiper (n = 109). The structural size of these birds, measured as wing length, didn't differ from the rest of birds (mean ± SD; Common Snipe: 137.1 ± 3.1 vs. 137.0 ± 4.0, t = 0.29, P = 0.77; Wood Sandpiper: 128.6 ± 3.49 vs. 128.2 ± 3.1; t = 1.17, P = 0.24), hence the groups were representative for the analyses.

### 2.2. Flight range estimates

The potential flight ranges of the species were estimated following three different approaches, expressed by the following formulas:

$$R = 163.24 \cdot S \cdot (M_2^{0.256} - M_1^{0.256}),$$

Summers & Waltner (1979) (1)

$$R = 95.447 \cdot S \cdot (M_2^{0.302} - M_1^{0.302}),$$

Davidson (1984) (2)

$$R = 26.88 \cdot S \cdot L^{1.614} \cdot (M_1^{-0.464} - M_2^{-0.464}),$$

Castro & Meyers (1989) (3)

where R is the flight range (in km), S the flight speed (in km/h), L the wing length (in cm),  $M_1$  the lean mass (in g),  $M_2$  the total mass (in g). The flight speed S = 13 m/s = 46.8 km/h was estimated as typical for migrating waders (Hedenström *et al.* 2002). The mean wing length was 13.71 cm for Common Snipe (n = 3,772) and 12.82 cm for

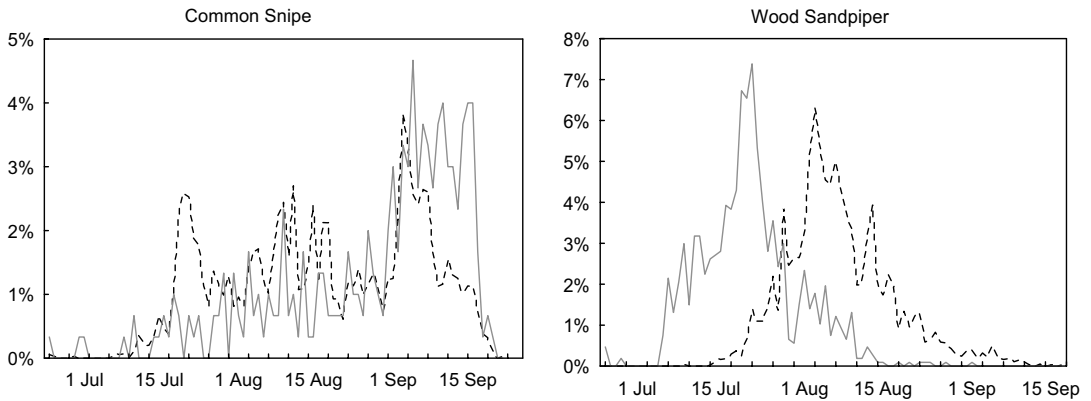


Fig. 1. Autumn migration phenology of Common Snipes and Wood Sandpipers. Juveniles are indicated with a dashed line, and adults with a solid line.

Wood Sandpiper ( $n = 4,686$ ). In all statistical analyses normality of distribution was checked where necessary. All statistical procedures were performed using STATISTICA 5.2 software according to Zar (1996).

### 3. Results

#### 3.1. Phenology

The migration waves of adult and juvenile Wood Sandpipers were clearly divided into two peaks (Fig. 1a). The first adult Wood Sandpipers were caught on 26 June. The juveniles usually appeared about two weeks later, with the first record on 10 July. A similar interval was noted between ringing the last birds from both age groups, with 3 September for adults, and 20 September for juveniles.

The Common Snipe showed no time separation between migration of adults and juveniles (Fig. 1b). The first Snipes from both age groups were caught at Jeziorsko on the same day of 25 June. Throughout the whole ringing period the percentage of banded adults and juveniles changed in a similar way. The last birds were caught on 21 (adult) and 23 (juvenile) September. However, it should be noted that fieldwork never covered the whole Snipe autumn migration through the study area (although it covered the main migration period).

#### 3.2. Moulting

Common Snipe was confirmed to undergo moulting during the autumn migration. Every season there was a considerable fraction of moulting birds recorded at Jeziorsko. In the years 2004–2005, approximately half of all Snipes showed signs of moulting. These moulting birds were noted through the whole period of fieldwork in similar frequencies (Fig. 2). In 2005, over 30% of adult Snipes were moulting flight-feathers. On the contrary, there were only two recorded Wood Sandpipers moulting flight-feathers. Each season very few Wood Sandpipers changing body-feathers in partial moults were caught and the fraction of such birds didn't exceed 1%.

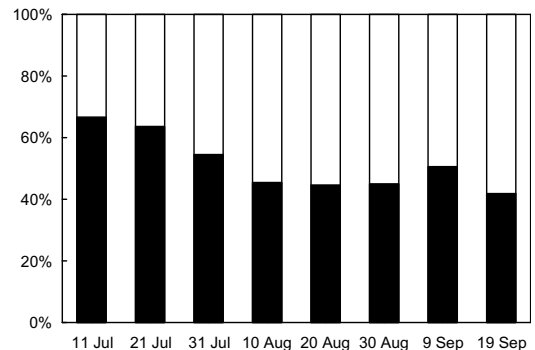


Fig. 2. Frequency of moulting Common Snipes during autumn migration at Jeziorsko reservoir in the year 2005.

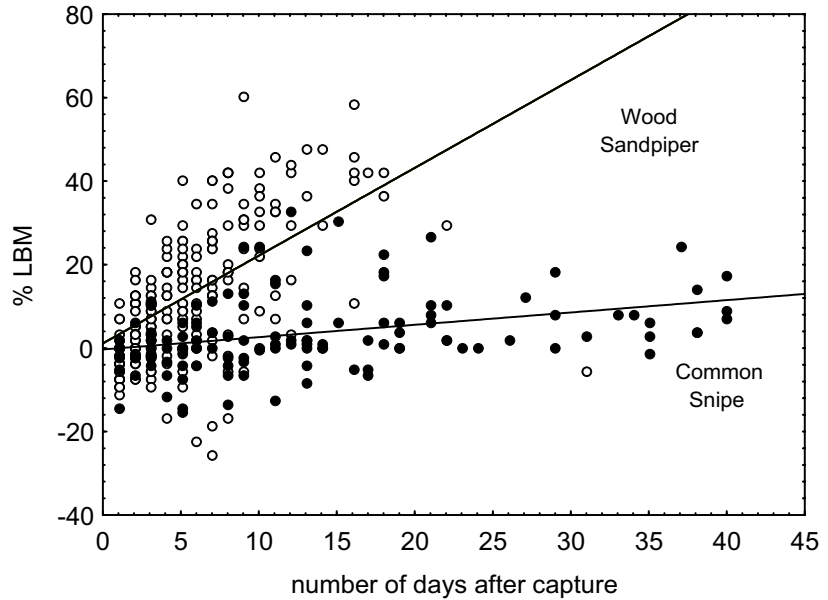


Fig. 3. Relationships between body-mass changes and the time of staying at the Jeziorsko reservoir for Common Snipes (black circles) and Wood Sandpipers (white circles).

**3.3. Body mass changes**

On average, Wood Sandpipers gained 1.15 g/day. The corresponding value for Snipes was lower and equalled 0.30 g/day. Relationships between body-mass changes (percent of LBM) and the time of staying at the stopover (number of days) were estimated for both species using linear regression (Fig. 3).

For Common Snipe, the relationship was  $\text{body-mass change} = 0.296 \cdot \text{number of days} - 0.338$  ( $R^2 = 0.11$ ,  $\text{SEE} = 8.45$ ,  $F_{1,125} = 16.85$ ,  $P < 0.001$ ). For Wood Sandpiper,  $\text{body-mass change} = 2.103 \cdot \text{number of days} + 1.114$  ( $R^2 = 0.33$ ,  $\text{SEE} = 13.01$ ,  $F_{1,222} = 108.31$ ,  $P < 0.001$ ).

The average percent of LBM gained by a bird per day at Jeziorsko (the slope coefficients estimated above) was significantly higher for Wood Sandpiper than for Common Snipe ( $t = 8.40$ ,  $P < 0.001$ ). Also the maximum observed weight gain was higher for Wood Sandpiper (5.67 g/day, 10.4% of LBM/day) than for Common Snipe (3.66 g/day, 3.76% of LBM/day). Wood Sandpiper showed a significant correlation between the length of stay at the reservoir and the fuelling rate ( $r = 0.21$ ,  $P = 0.001$ ,  $n = 226$ ). In contrast, Common Snipes stayed at the stopover site independent of the rate of fat accumulation ( $r = 0.12$ ,  $P = 0.148$ ,  $n = 149$ ).

**3.4. Length of stay**

Median lengths of stay were 5 days for Wood Sandpipers and 11 days for Common Snipes ( $Z = 8.12$ ,  $P < 0.001$ ,  $n_1 = 227$ ,  $n_2 = 139$ ; Fig. 4). The

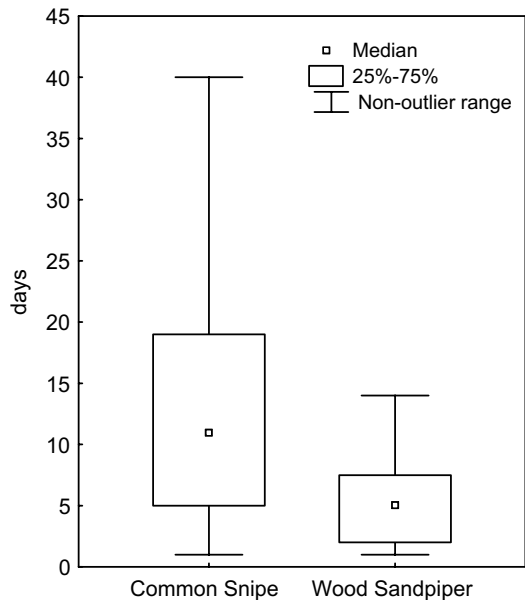


Fig. 4. Median length of stay at Jeziorsko reservoir for Common Snipe and Wood Sandpiper.

Table 1. Potential flight ranges of Common Snipe and Wood Sandpiper caught at the Jeziorsko reservoir during autumn migration. Distances (in km) are estimated according to different methods, as explained in the Material and methods section.

Method	Common Snipe	Wood Sandpiper	t	P
<i>Birds with non-zero fat load</i>				
Summers & Waltner (1979)	344	1,101	35.5	<0.001
Davidson (1984)	295	919	34.8	<0.001
Castro & Meyers (1989)	238	1,022	43.2	<0.001
<i>The heaviest 10% of birds</i>				
Summers & Waltner (1979)	1,508	2,649	44.4	<0.001
Davidson (1984)	1,290	2,220	42.2	<0.001
Castro & Meyers (1989)	1,043	2,320	73.3	<0.001

maximum recorded periods of staying at the site were 31 and 42 days, respectively.

### 3.5. Flight range

Common Snipes had significantly smaller (4% of LBM) mean fuel loads than Wood Sandpipers (21% of LBM;  $t = 44.86$ ,  $P < 0.001$ ). Similar results were obtained for maximum fuel loads, which were 54% and 81%, respectively. The theoretical flight ranges differed dramatically between the species (Table 1). In all cases, Wood Sandpipers, which accumulated more fat reserves at Jeziorsko, had significantly higher mean flight ranges than Common Snipes. Also the flight ranges of individuals with maximum fuel loads were highest for Wood Sandpipers, and they varied, depending on the equation used, between 2,925 and 3,512 km. The values for Common Snipes were between 1,884 and 2,919 km.

## 4. Discussion

### 4.1. Migration strategies at the Jeziorsko stopover site

Common Snipes and Wood Sandpipers using Jeziorsko reservoir as a stopover site during autumn migration show different life history and migration strategies. Life-history differences are apparent in the phenology of migration of adults and juveniles, where only Wood Sandpipers show a clear division in the timing of autumn migration

between these age groups. Such separation was also observed at other stopover sites at the coast or on inland water bodies (Glutz von Blotzheim *et al.* 1977, Meissner 1997a, Gromadzka 1989, Mitrus *et al.* 1998). This pattern is also typical for many other waders, mainly *Calidris* and *Tringa* species. Two migration peaks are observed in S-strategy representatives (Alerstam & Högstedt 1982). In species whose numbers are limited by carrying capacities of breeding grounds, adults try to leave such unprofitable areas as quickly as possible when parental care for offspring is finished. Juveniles stay longer to finish growth and prepare for migration. This results in two migration waves, the first consisting of adult birds which are subsequently followed by juveniles. In contrast to this pattern, both age groups are present at Jeziorsko during the whole Common Snipe migration period.

Such a pattern is typical for B-species (Alerstam & Högstedt 1982, Meltotte 1996). It's not advantageous for these birds to leave their breeding grounds quickly, as intraspecific competition is pronounced mainly at wintering areas, hence they try to prolong migration and reach wintering places only when the weather or feeding conditions on the route worsen markedly. Such conditions start at Jeziorsko between October and November, months when Common Snipes leave the reservoir (Janiszewski *et al.* 1998).

The theoretical assumptions indicate that S-species should shorten their length of migration to the minimum. This imposes a necessity of utilizing all energy stores on account of migration. Therefore, other energy consuming activities such as

Table 2. Length of stay and refueling speed of Wood Sandpipers and Common Snipes at different refueling sites in Europe as presented in the literature. Absence of information is indicated by dashes.

Site	Length of stay (days)	Refueling speed (g/day)	Source
<i>Wood Sandpiper</i>			
Sweden	–	1.15	Persson (1998)
Gulf of Gdansk	2.6–4.7	–	Meissner (1997a)
Ukraine	–	0.96	Szydłowski & Lysaczuk (1998)
Austria	4.5–5	–	Wichmann <i>et al.</i> (2004)
Greece (spring)	–	1.19	Akriotis (1991)
Italy	12.3	–	Sceba & Moschetti (1996)
<i>Common Snipe</i>			
Germany	13	~ 0	OAG Münster (1975)
Gulf of Gdansk	5–8	1.1	Meissner (2003)

moult should be separated from migration in time. Wood Sandpipers undergo post-breeding moult at wintering grounds in Africa (Cramp & Simmons 1996). Examples of birds moulting flight feathers in central Europe are extremely rare. From more than 1,000 adults caught at Jeziorsko, only two were moulting flight feathers. Similar situations were observed at stopover sites in the Prypiat river valley (in Belarus) and the Gulf of Gdansk or Wisla River valley in Poland (P. Pinczuk, M. Remisiewicz pers. comm.). On the contrary, adults moulting flight feathers comprise up to 30% of Common Snipes ringed at Jeziorsko. A similar pattern was observed in Germany and Belarus (OAG Münster 1975, Pinczuk pers. comm.). Most Common Snipes ringed at a Münster sewage farm had started their wing moult before reaching Germany (OAG Münster 1975). This species begins post-breeding moult at breeding grounds or at the onset of migration.

#### 4.2. Migration duration and staying time

It's believed that the distance travelled during migration belongs to factors that determine moulting period (Holmes 1971). Waders wintering in western Europe start moulting at breeding grounds or at the beginning of migration in order to finish before harsh winter conditions come (Meltofte 1996). Such a strategy has been observed in Dunlins *Calidris alpina* and, to some extent, Purple Sandpiper *Calidris maritima* (Holmes 1966, Summers *et al.* 2004). Dunlins from Siberia and Alaska win-

tering close to their breeding grounds start their moulting period very early, even during incubation (Holmes 1966, Gromadzka 1989). The same was observed in Purple Sandpipers breeding in Russia or Svalbard and wintering in Norway (Summers *et al.* 2004). On the contrary, Little Stints *Calidris minuta*, Curlew Sandpipers *Calidris ferruginea* and Wood Sandpipers flying long distances between Arctic breeding grounds and wintering areas in southern Africa moult after migration (Middlemiss 1961, Elliott *et al.* 1976, Meltofte 1996). Since Common Snipes migrate slowly in small jumps they should be able to cope with energy expenditure created by flight and moult occurring at the same time. Some specimens ringed at Jeziorsko had gaps in their wings caused by shedding of secondaries, which considerably worsens flight performance (Włodarczyk *et al.* 2005). Such impairment would definitely prevent birds from travelling long distances in one single flight.

However, short journeys by moulting birds are nothing extraordinary. There were no negative effects of moult on flying ability in Tree Sparrow *Passer montanus* and Starling *Sturnus vulgaris* (Lind 2001, Williams & Swaddle 2003). Grey Plovers *Pluvialis squatarola* showed simultaneous moult and preflight mass increase, which suggests low energetic costs of moult, at least in this species (Serra *et al.* 2006). These findings support the notion that the period of autumn passage doesn't have to be separated in time from the period of moult in species migrating in small steps.

We found that Wood Sandpipers had shorter

stays on the stopover site than Common Snipes. The staying time of these species varies across sites in Europe (Table 2), although the pattern of shorter stays in Wood Sandpipers generally seems to hold. The hypothesis of quick Wood Sandpiper turnover at Jeziorsko is supported by colour-ringing. In the years 1999–2002 more than 800 individuals were individually colour ringed within the project *Tringa glareola* 2000 (Remisiewicz 1998). Despite this, we obtained less than 10 resightings in the same season, all within 1–2 days after ringing. The same stay length of Wood Sandpiper (4.5–5 days) was observed in Austria (Table 2, Wichmann *et al.* 2004). At the stopover site in Italy birds stayed longer, 12.3 days on average (Scebba & Moschetti 1996). Nevertheless, this result was based on only six retrappings, from which three birds stayed 6–8 days.

Moreover, it's supposed that Wood Sandpipers use wetlands along the Mediterranean Sea as last refuelling sites before direct flights to central Africa (Cramp & Simmons 1986). Hence they need more time to accumulate enough fat for such long constant flight. Wood Sandpipers using the Gulf of Gdansk as a stopover site stay for 2.6–4.7 days, depending on the site (Meissner 1997a). Median length of stay of Common Snipe within the same area was longer, equalling 5–8 days (Meissner 2003). The corresponding value for birds ringed at the sewage plant in Münster was even longer, 13 days (OAG Münster 1975).

Common Snipes and Wood Sandpipers meet at Jeziorsko the same feeding conditions as they use the same feeding areas (muddy beaches created when the reservoir is being emptied of water). The regular water level cycle creates abundant food supply renewable every few days. The water level drops constantly from 3.5 m to 2.5 m over a four month period (June–October). Despite foraging under the same conditions, the species show different refuelling rates. Estimated mean energy gain of Wood Sandpiper is 1.15 g/day, whereas for Common Snipe it was only 0.3 g/day. These values are consistent with results obtained in other parts of Europe (Table 2). Common Snipes caught at other stopover sites during southward migration reflect weight loss or marginal gain of fat. A German study detected mainly weight loss in retrapped individuals (OAG Münster 1975). At Jastarnia, in the Gulf of Gdansk, retrapped Com-

mon Snipes showed no change in body mass (Meissner 2003). However, data from three different locations within the Gulf of Gdansk showed weight gain for retrapped birds on the level of 1.1 g/day (Meissner 2003). This calculation was based only on birds that gained weight. Using the same procedure, we obtained a refuelling rate of 0.9 g/day at Jeziorsko, a value similar to the Gulf of Gdansk area.

Both species differ in their departure decisions. Wood Sandpipers stay longer if they can gain considerable fat reserves in a short time period, and we found a positive correlation between stay length and refuelling rate. When the possibility of fat accumulation at the reservoir is not satisfactory birds may move to another stopover site where they might find more profitable feeding conditions, and thus lower the overall migration time. In contrast, Common Snipes leave the reservoir after a given period of time, independently of refuelling rate. This difference is consistent with differences between time- and energy-minimization strategy models proposed by Alerstam and Lindström (1990). A similar pattern for Wood Sandpipers was observed at the Gulf of Gdańsk where birds didn't stop accumulating fat on any defined level (Meissner 1997a). However, the majority of birds passing the Gulf of Gdańsk didn't accumulate large amounts of fat as in the energy minimization strategy. This could be the result of unpredictability in changes of food resources at the refuelling site (Meissner 1997a).

Wood Sandpipers rest at Jeziorsko reservoir for shorter times and accumulate fat at higher rates than Common Snipes. Moreover, they stay at Jeziorsko longer if the refuelling rate is high. Many other waders thought to be time-minimizers behave analogously. Red Knot *Calidris canutus*, a fast migrant travelling long distances from breeding grounds in Siberia to wintering grounds in Africa, shows a mean refuelling rate of about 2.5 g/day (2.8% of LBM/day) (Nebel *et al.* 2000, Helseth *et al.* 2005). Curlew Sandpipers *Calidris ferruginea*, passing central Europe during southward migration to wintering grounds in Africa, show refuelling rates of 1.7–2.1 g/day according to age class (Meissner & Górecki 2006). This species during spring migration accumulates fat with a similar rate of 2.8 g/day (Scebba & Moschetti 2006). Common Snipes passing through Jeziorsko



revealed a small rate of weight gain, long resting duration and lack of correlation between refuelling rate and stay length. All mentioned features suggest an energy minimizing strategy. Waders are generally known for high refuelling rates during migration (Lindström 1991). Maximum fat gain observed at Jeziorsko for Common Snipe (3.4% of LBM/day) was much lower than maximum values observed in the majority of waders (5–9% of LBM/day) (Lindström 1991).

Few studies revealed migration with low refuelling ratios in this group of birds. Dunlins caught at the British coast during northward migration showed similar low fat gain (0.57 g/day) (Eades & Okill 1977). However, these birds had already large fat reserves (up to 30% of LBM), which could result in slow refuelling rate. Moreover, this species shows an inverse relationship between the length of stay at a particular site and refuelling rate. Juvenile dunlins staying up to four days in the Rewa region (Baltic coast, Poland) gained 1.74 g/day whereas birds staying over eight days gained only 0.42 g/day (Meissner 1998). Dunlins from the Rewa region fly to their wintering grounds in western Europe along the coast. Other birds wintering in the Black Sea area use inland water bodies as resting places. Neither group travels long distances or crosses any large geographical barriers. As a result, they migrate according to the energy minimization strategy.

Also Common Sandpipers and the majority of Wood Sandpipers using the Gulf of Gdansk as a refuelling site seem to be energy minimizers (Meissner 1997a, 1997b). The Baltic coast, with unpredictable winds influencing access to food for waders, seems to be, at least temporarily, of poor quality for them. Therefore, Sandpipers are often forced to leave the area with low fat reserves, enabling birds to cover only short distances to the nearest more profitable wetland. Such a migration strategy was the result of poor feeding conditions. At Jeziorsko reservoir food resources are abundant during the whole migration period. This further supports the conclusion that Common Snipes use an energy minimization strategy even in areas where a quick refuelling rate is possible.

Additional to quicker refuelling rates, Wood Sandpipers show higher mean and maximum fuel loads than Common Snipes, and leave the reservoir with at least five times larger fat loads than

Common Snipes. Studies of Wood Sandpipers during autumn migration in Austria showed similar maximum fuel loads, reaching 88% of LBM in adults and 67% of LBM in juveniles (Wichmann *et al.* 2004). Temminck's Stints *Calidris temminckii*, wintering in central Africa, show similar large fat loads while passing southern Sweden (mean 21–32% of LBM, max. 75–81% of LBM; Hedenström 2004). Another example of an S-strategist which accumulates even higher fat reserves is the Red Knot. Spring migration of this species covers a few thousand kilometres between western Europe and breeding grounds in northeastern Siberia.

This kind of exertion requires extremely high energy expenditure, which is satisfied with a mean fat load of about 60% of LBM, as assessed for birds in Morecombe Bay (United Kingdom) in the end of April (Prater 1972, 1974). Birds ringed at the Baltic coast during southward migration showed lower fat loads of 13–14% of LBM. However, the maximum value (77% of LBM) was similar (Helseth *et al.* 2005). Data about fat content estimation for Common Snipe are scarce and don't allow comparing our results with other resting areas. However, the pattern observed in this species is completely different from the Wood Sandpiper. For example, Common Snipes ringed at the Polish coast showed, on average, weight close to the value of LBM calculated in this study, which suggests extremely low fat reserves (approximately 1% of LBM) (Meissner 2003).

### 4.3. Inferred migration distances and route

Fat load influences the theoretical flight range of individuals. These results should be analysed with caution due to large discrepancies between three theoretical methods (Table 1). Nevertheless, larger amounts of fat permit longer distances to be covered. Taking into consideration the heaviest 10% of birds, which Davidson (1984) suggested to be appropriate for flight range analyses, would allow Wood Sandpipers leaving Jeziorsko during autumn migration to fly constantly 2,200–2,600 km. On the other hand, Wood Sandpipers caught further south revealed larger fat reserves and slightly longer mean flight ranges between 2,500–4,500 km (Wichmann *et al.* 2004). Analysis of recoveries from birds ringed at Jeziorsko shows a

lack of resightings from central Europe (Germany, Austria, Czech Republic) during the autumn migration. This is even more striking considering that in 1999–2003 an intensive ringing scheme along the migratory flyway of the species took place within the project *Tringa glareola* 2000. Colour-ringing activity at Jeziorsko gave no recoveries from central Europe.

It suggests that individuals using Jeziorsko fly directly to the coast of the Mediterranean Sea or even cross it. This is supported by the recovery of an adult bird, ringed in August and recaptured after nine days in northern Italy. The distance the bird covered in such a short period of time equalled 950 km, nearly the mean value for Wood Sandpipers staying at Jeziorsko (Table 1). Common Snipes leaving Jeziorsko can fly up to 1,000–1,500 km, significantly less than estimates for Wood Sandpipers. Such a flight distance is enough to reach the western border of its wintering grounds. However, the mean distance for birds ringed at Jeziorsko is much smaller (200–300 km). Distance estimated for the heaviest birds is not consistent with assumptions of the energy minimization strategy (short distances covered in one flight and many refuelling sites along the route).

Furthermore, values estimated for all birds with non-zero fat loads support the energy minimization strategy as birds have to use 3–4 additional stopover sites to reach their wintering areas. This difference shows that obtained distances are highly theoretical and should be used carefully. Only direct recoveries can give some insight into speed of migration. During 18 years of studies we obtained more than 150 recoveries, all from wintering grounds (France, Spain, Italy). Moreover, all birds were shot at least 20 days after ringing. This situation is also observed at other ringing stations (W. Meissner, P. Pinczuk, A. Seeger pers. comm.). Despite the equal distribution of ringing points throughout central Europe and intensive field work in Germany, there are no recaptures of birds ringed in Poland (U. Koeppen, pers. comm.).

Such a situation could be connected with a large number of passing compared to marked birds and unusually high mortality within wintering grounds caused by hunting. The first assumption seems to be true since, despite intensive ringing at Jeziorsko with up to 200–600 birds ringed annually, numbers of controls reach 0–2 birds each sea-

son. Secondly, in France, Spain and Italy Common Snipe is an important game bird, whereas in Germany and Poland it's protected (Rouxel 2000). More than 95% of all known causes of mortality of ringed birds are attributed to hunters (Henderson *et al.* 1993). Hunting bags at wintering grounds are estimated on the level of about 1 million birds per year, which obviously influences the number and localization of recoveries (Devort *et al.* 1997). There is only one direct recovery of a bird ringed in Belarus (Turov) and recaptured after 6 days at Jeziorsko. The distance travelled was 623 km but this bird arrived at rather than left Jeziorsko.

In conclusion, differences between Wood Sandpiper and Common Snipe in the time they stay to forage and the refuelling rate at Jeziorsko reservoir support criteria for treating the former as representative of the S-strategy and the latter of the B-strategy. Moreover, migration behaviour of Wood Sandpipers at Jeziorsko supports a time-selected strategy whereas the behaviour of the Common Snipe suggests an energy minimization strategy.

### **Lirojen ja taivaanvuohien erilaiset syysmuuttostrategiat**

Kahlaajat valitsevat pääasiassa kahden erilaisen muuttostrategian väliltä syksyisellä matkallaan talvehtimisalueille. Energiankulutuksen minimointiin tähtäävän strategian valinneet lajit aloittavat sulkasadon jo pesimäalueilla. Pesimäseuduiltaan ne lähtevät syysmuutolle myöhään ja siirtyvät talvehtimisalueille pysähtyen usein matkallaan syömään ja lepäämään. Toinen pääasiallinen strategia on minimoida muuttoon kuluva aika. Lajit, jotka noudattavat tätä strategiaa, pysähtyvät muuttomatallaan vain muutamalla paikalla lepäämään ja ”tankkaamaan”, sekä sulkevat vasta talvehtimisalueillaan.

Lirojen ja taivaanvuohien syysmuuttoa tutkittiin Puolan Jeziorskon luonnonpuistossa. Aikuiset ja nuoret lirot muuttivat eri aikoina, eivätkä pyydystetyt linnut olleet aloittaneet sulkasatoaan. Sen sijaan sekä aikuiset että nuoret taivaanvuohet muuttivat samoihin aikoihin ja 30 % aikuisista taivaanvuohista oli jo aloittanut sulkasadon tutkimusalueelle saapuessaan. Lirot pysähtyivät tutkimusalueella 4–5 päivän ajaksi ja lihoivat taukonsa

aikana 1.15 g päivää kohden. Lähtiessään lirojen rasvaprosentti oli 17.4. Tällainen vararavinnon määrä mahdollistaa jopa 2 500 km:n muuttomatkan Välimeren rannikolle.

Taivaanvuohet sen sijaan pysähtyivät keskimäärin 11 päiväksi ja lihoivat 0.3 g päivässä. Ne myös lähtivät tutkimusalueelta riippumatta rasvaprosentin suuruudesta. Taivaanvuohien rasvavarastot olivat selvästi lirojen vastaavia pienemmät ja niiden arvioitiin riittävän maksimissaan 1 500 km:n lentomatkaan. Tuloksienne mukaan taivaanvuohet minimoivat muuttomatallaan kuluttamansa energian, kun taas lirot pyrkivät minimoimaan muuttomatkiaan kuluvan ajan.

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