Age-related stopover strategies in the Wood Sandpiper *Tringa glareola*

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Wood Sandpipers have been trapped between the years 2000 and 2003 during their autumn migration at Hohenau, in the north-east of Austria. Birds seem to deposit fat reserves continually throughout a small step migration across Central Europe; hence Wood Sandpipers need a large number of stopover sites to continue migration. Fat score of the birds increases as the season progresses at Hohenau, which may be an insurance against any deterioration of food supply as the time available for migration decreases. Strong evidence was found that adults and juveniles use different migration strategies: adults possessing higher body mass and thus carrying higher fat loads than juveniles. The juveniles are therefore forced to spend more time feeding and in consequence are more vulnerable both to a deterioration of food supply and to predation. Juveniles seem to avoid competition with each other. Transient juveniles may be adapted to migrate in longer stages than temporary residents. Potential flight ranges were calculated, suggesting that most of the birds, especially the juveniles, need additional staging sites before crossing the Mediterranean Sea and the Sahara.

1. Introduction

Birds migrating from their northern hemisphere breeding grounds to their African wintering quarters are confronted with a number of wide ecological barriers; namely the Alps, the Mediterranean Sea and the Sahara. Waders in particular carry out long-distance flights and therefore need sufficient fat reserves to cross these barriers (Alerstam & Lindström 1990, Biebach & Bauchinger 2003, Lindström 2003). A variety of migration strategies have been evolved to deal successfully with the long journey and the associated energy-demands (Pienkowski & Evans 1984, Evans & Davidson 1990). Alerstam and Lindström (1990) distin-

guished two selective forces as being responsible for the evolution of migration strategies: time and energy. As migrating birds are not able to minimise both pressures simultaneously, migrants can be classified as 'time-minimisers' or 'energy-minimisers' (Alerstam & Lindström 1990). Predators also constitute a significant hazard to migrants, perhaps compromising their ability to minimise time or energy effectively in those areas with a high risk of predation (Lank *et al.* 2003).

Because the selective forces acting on individuals can vary in regard to the different sexes, different populations, or different age classes, the result can be an intraspecific differentiation in migration strategies. Juvenile American Redstarts

Setophaga ruticilla, for example, are behaviourally subordinate to adults on migration (Woodrey 2000) and have deposited less fat when captured during their autumn stopover at the Gulf of Mexico (Woodrey & Moore 1997). Younger birds are forced to stay longer at the stopover sites to accumulate sufficient fat reserves for migration (Moore *et al.* 2003). Another example is provided by Townshend (1985), who showed how juvenile Grey Plovers *Pluvialis squatarola* were displaced in autumn from a possible wintering post after unsuccessful competition with adults or with other juveniles for feeding sites. Juveniles that were displaced were usually smaller-sized birds that were adapted to travel further, or larger juveniles that failed to compete successfully with adults. These examples give some evidence that juvenile birds can be exposed to a higher rate of competition or are less experienced in foraging and are forced to use different migration strategies from adults.

The data presented here were collected during the course of the international project 'Tringa glareola 2000', co-ordinated by the KULING Waterbird Research Group, under the auspices of the Wader Study Group. The aim of the project is to improve the knowledge of Wood Sandpiper migration through Europe and Africa, in particular the aspects of spring and autumn migration: such as core areas, phenology, migration dynamics and migratory strategies (cf. Remisiewicz 1997). Within this international network Wood Sandpipers were caught at Hohenau during autumn migration and we found evidence of age-related stopover strategies in the species. To give a general idea about the migration pattern of Wood Sandpipers in autumn, we will first summarise the current knowledge of this topic, and then discuss our findings in the light of both the migration strategy used by Wood Sandpipers and of migration strategies in general.

2. Study Area

The 'Absetzbecken Hohenau-Ringelsdorf' (48°35'N, 16°55'E) lie almost at the confluence of the rivers March/Morava and Thaya/Dyje in north-east Austria, where the borders of the Czech Republic, Slovakia and Austria meet. The site consists of a set of small, disused, mud-settling la-

goons ('Anlandebecken' – total area 38 ha) from the nearby sugar factory, along with a 17 hectare pool ('Kühlteich') used for cooling water emitted during the winter's sugar processing. The site is managed primarily for wetland birds and contains a mosaic of shallow water, wet vegetation and muddy areas (Zuna-Kratky *et al.* 2000). Wood Sandpipers are characteristic and numerous visitors to the area, in lower numbers in spring than in autumn, with daily counts regularly exceeding 100 individuals in autumn and a peak count of 234 individuals (Zuna-Kratky *et al.* 2000, Wichmann *et al.* 2002).

3. Methods

Since the year 2000, small numbers of autumn migrant Wood Sandpipers have been caught at the Hohenau Absetzbecken in July and August. On the shallow flooded pools of the Anlandebecken birds were caught with mistnets and with 9 walk-in wader traps – similar to those described in Meissner (1998) – placed around the shorelines of the pools. Trapping was carried out from Friday until Monday, dawn to dusk each day. While mistnets were controlled every hour, walk-in-traps were checked in a 2-hour cycle. The birds were ringed and colour-marked, and measurements taken as follows: flattened, straightened wing to an accuracy of 0.5 mm and bill to skull (BTS) to 0.1 mm, both measured as in Prater *et al.* (1977). The birds were also weighed with an electric balance to an accuracy of 0.1 grams. All birds were aged following the guidelines in Prater *et al.* (1977), using feather wear, particularly on scapulars and remiges, and above all the colour of the upperpart markings to distinguish adults from juveniles. The first author did approximately 60% of the measurements, with most of the remaining measurements being double-checked.

Fat score was assessed in accordance with the Kaiser scale (Kaiser 1993) as an index of condition. This fat-scoring method estimates the subcutaneous fat deposits of a bird. To determine this, two of the most important visible fat deposits are checked: one in the furcular depression, the other on the abdomen. Instead of the 31 classes proposed by Kaiser (1993), we used 16 classes – Kaiser's 9 main classes and 7 additional subclasses –

to determine the amount of visible fat. We considered Kaiser's fat-scoring method to be the most accurate index of condition, as in contrast to body mass, fat score is independent of either the size of the bird or the time of capture. Fat score should also minimise the effect of structural size (larger birds are physically capable of carrying a heavier fat load), as fat score correlates strongly with actual fat content (Kaiser 1993). The dimension of the pectoral muscle was estimated according to Bairlein (1995). Muscle shape was divided into 4 main classes (0–3). To obtain a finer scale 3 subclasses were added. Class 0 was used for birds showing a sunken muscle; class 1 was used for pectoral muscles resembling a straight line to the sternum. If the sternum was barely perceptible with the thumb (typical of migrating birds), the muscle was classified as 2. None of the birds had pectoral muscle exceeding class 2.

Because birds were trapped in mist nets and walk-in-traps we checked for any influence of capture method on body mass or fat score. Neither adults nor juveniles showed differences in body mass that could be attributed to capture method (adults: $U = 1815.0$, $P = 0.21$, $n_1 = 32$, $n_2 = 48$, juveniles: $U = 1536.5$, $P = 0.23$, $n_1 = 24$, $n_2 = 46$). Fat score was also independent of capture method (adults: $U = 1247.5$, $P = 0.63$, $n_1 = 32$, $n_2 = 48$, juveniles: $U = 1619.5$, $P = 0.87$, $n_1 = 24$, $n_2 = 46$). Data of birds caught in mist nets and walk-in-traps were therefore pooled. Due to the small sample of birds retrapped (6) we cannot say anything about body mass changes.

80 adults and 66 juveniles were caught in total, of which 38 adults and 36 juveniles were marked individually (Table 1). Individual ringing of juveniles took place in 2002 and 2003, whereas adults were only marked individually in 2003. The observed duration of stay is an estimate of minimum length of stay, as generally birds are not captured directly after arrival. Birds remaining more than 1 day at the site are termed 'temporary residents' (cf. Lyons & Haig 1995). Birds that were not resighted after marking ('transients'), apparently leaving the area on the day of capture, were excluded from analyses of minimum length of stay.

The behaviour of the birds was also assessed using a 20×–60× telescope, so that age classes could be separated. On an hourly basis every Wood Sandpiper was counted and its behaviour

Table 1. Numbers of Wood Sandpipers ringed at the Absetzbecken Hohenau-Ringelsdorf from 2000–2003.

Year	2000	2001	2002	2003	Sum
Adults	9	15	18	38	80
Juveniles	20	7	28	11	66

recorded either as foraging, resting (including preening and bathing), watching for predators ('scanning') or competitive behaviour ('fighting'). The time of day was adjusted to sunrise for the analyses, and the day divided into morning (1 to 5 h after sunrise), midday (6 to 10 h) and evening (11 to 15 h). Between the hourly counts ('scan sampling'), individually marked birds were sought out and watched for five consecutive minutes, recording the same behavioural details at 15 s intervals ('focal sampling'). In all, 56 records of juveniles, and 11 records of adults were made.

We calculated the potential flight ranges of Wood Sandpipers at first capture, using Castro and Myers' (1989) formula and assuming an average flight speed of 60 km/h (Persson 1998, Zwarts *et al.* 1990):

eq. 1: $R = 26.88 \ S \ WL^{1.614}(LM^{-0.464} - M^{-0.464})$

where R = flight range (km), S = flight speed (km/h), WL = wing length (cm), LM = lean mass (g), M = actual body mass (g).

Lean mass was computed using the formulae in Davidson (1983):

eq. 2: Adults: $LM = (0.028WL + 0.032)^3$

eq. 3: Juveniles: $LM = (0.030WL - 0.132)^3$

where LM = lean mass (g), WL = wing length (mm), 1 SE (eq. 2 and 3.) $= LM^{0.33} = 0.18$.

As Davidson (1984) proposed, potential flight range was calculated for the heaviest 10% of the Wood Sandpipers, as they are the most likely to be ready for departure. Mean wing length and mean body mass of these birds was used to compute the lean mass in eq. 2 and 3 (Davidson 1983). We ascertained the fat load (dissimilar to the fat score) of the birds by subtracting lean mass from actual mass.

For the purposes of data analysis, Mann-Whitney-U-test, χ^2-test, Spearman-Rank correlation, linear regression analyses and ANCOVA were used. To avoid violation of the assumptions of linear regression models, such as normal distribution or homogeneity of variance, the significance of linear regression analyses was tested by randomisation: 3,000 permutations were carried out using a program from H. Nemeschkal (University of Vienna). The scan sampling data of behavioural activity was analysed by means of ANCOVA. The proportion of time that birds spent in different activities (dependant variable) was arcsin-transformed. Age of the birds and time of day were the independent variables and treated as categorical variables. As behaviour changed during the season, time of year was used as continuous covariate. Significance was assessed by means of bootstrap. 3,000 permutations were performed using SIMSTAT 2.5. Results of hypothesis tests were considered statistically significant if P < 0.05.

4. Results

4.1. Age classes

Body mass correlates significantly with fat score for the birds trapped at Hohenau (Spearman: r_s = 0.88, P < 0.001, n = 140). We therefore used fat score to analyse the condition of the birds. Size of fat deposit was significantly larger in adults than in juveniles (U = 2019, P = 0.025, n_1 = 76, n_2 = 64,
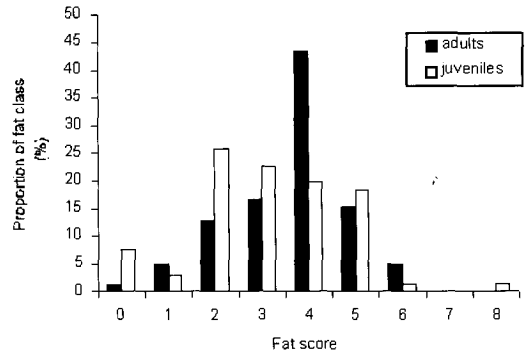

Fig. 1. Differences in fat score between adult and juvenile Wood Sandpipers caught at the Absetzbecken Hohenau-Ringelsdorf, using the Kaiser scale (1993).

Fig. 1), and adults also weighed significantly more than juveniles (U = 1861.5, P = 0.017, n_1 = 76, n_2 = 64, Table 2). Adults and juveniles showed a slight but significant increase in fat score at first capture as the season progressed (adults: y = 0.18x – 3.76, r^2 = 0.10, P < 0.01, n = 76, juveniles: y = 0.34x – 11.78, r^2 = 0.14, P < 0.01, n = 64, Fig. 2).

4.2. Residents and transients

When comparing the numbers of temporary residents and transients, we found no differences between 2002 and 2003 (χ^2 = 0.323, P > 0.05). Juveniles showed a significantly higher proportion of temporary residency than adults (50% and 31.6% respectively, χ^2 = 10.22, P < 0.001). In Table 3 the

Table 2. Body mass ranges (g) of Wood Sandpipers trapped at Hohenau, NE Austria during autumn migration, compared with other sites on the Black Sea/Mediterranean Flyway. Sites are ordered by decreasing latitude.

| Site	Adults Mean(± SD)	n	Juveniles Mean(± SD)	n
Gdansk, Poland (Meissner 1997) 54°30–42'N, 18°30–40'E			59.8 (± 8.0)	743
Bug River, C-Poland (Mintus et al. 1998) 52°17'N, 22°31'E	58.7 (± 8.9)	102	59.2 (± 8.0)	426
Cholginii, W-Ukraine (Szydlowski & Lysaczuk 1998) 49°56'N, 23°26'E			64.7 (± 0.5)	393
Hohenau, Austria 48°35'N, 16°55'E	69.4 (± 8.3)	78	65.9 (± 8.9)	66
Ägelsee, Switzerland (Leuzinger & Jenni 1993)	68.3 (± 8.6)	187	67.0 (± 9.5)	525
Volturno Plain, S-Italy (Scebba & Moschetti 1996)	72.5 (±9.3)	98	66.9 (± 11.5)	98
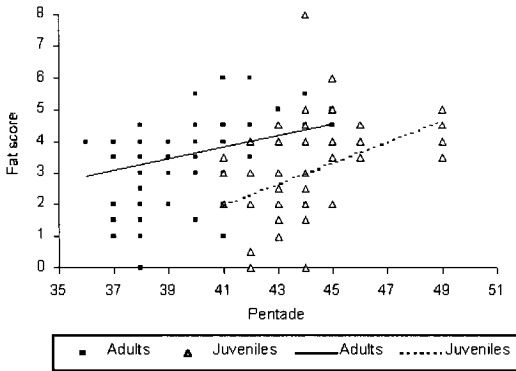
Fig. 2. Fat score at ringing related to pentade ringed (Pentade 35 = June 20th–24th).

biometry of transients and temporary residents is listed and the data were checked for differences. Whilst in adults the biometry of transients and temporary residents was similar, we found differences between transient and temporary resident juveniles. Transient juveniles had significantly shorter bill-to-skull lengths, and the pectoral muscle was more pronounced than in temporary residents.

4.3. Length of stay

56.8% of the 74 individually marked Wood Sandpipers (including transients) were re-sighted. 66.7% of the 36 juveniles, and 47.4% of the 38 adults were seen again; the high percentage of re-sightings is probably due to the small extent of the area. There was no significant difference in the length of time spent at the site by either age-class: the median length of stay being 4.5 days for juveniles and 5 days for adults (U = 81.5, P = 0.27, n_1 = 18, n_2 = 12). For juveniles the minimum length of stay was equal between years (U = 36.0, P = 0.73, n_1 = 9, n_2 = 9). Differences between years could not be tested for adults, as they were marked individually only in 2003. Whilst 50% of juveniles remained longer than 1 day at Hohenau, the percentage of adults was lower, at 36.1%. There is no apparent relationship between the minimum length of stay and the lateness of the season for adults (y = 0.06x + 39.44, r^2 = 0.07, P > 0.05, n = 13). Juveniles tended to shorten their minimum length of stay towards the end of the season, but the regression was not significant (y = –0.07x + 43.97, r^2 = 0.20, P = 0.06, n = 18). We found no correlation between fat score and minimum length of stay for either adults or juveniles (adults: y = –0.01x + 8.64,

Table 3. Biometry of temporary residents (n = 12, juv: n=18) and transients (n = 25, juv: n=21) migrating through Hohenau (see methods for classification of fat score and pectoral muscle). Differences were tested with Mann-Whitney U-Test.

Adults	Temporary residents		Transients			
	mean (± SD)	median	mean (± SD)	median	U-value	P
Wing length (mm)	126.0(± 3.8)	126.3	125.0 (± 4.0)	125.5	137.5	0.689
Bill to skull (mm)	29.8 (± 2.1)	29.2	29.9 (± 1.8)	29.7	130.5	0.532
Fat score	3.8 (± 1.4)	4.0	3.7 (± 1.0)	4.0	132.0	0.575
Pectoral muscle	0.9 (± 0.3)	1.0	0.9 (± 0.2)	1.0	146.0	0.911
Body mass (g)	69.8 (± 8.1)	69.0	68.6 (± 7.2)	68.9	135.0	0.643

Juveniles	Temporary residents		Transients			
	mean (± SD)	median	mean (± SD)	median	U-value	P
Wing length (mm)	127.3 (± 2.1)	127.0	127.0 (± 4.2)	127.0	164.0	0.685
Bill to skull (mm)	31.4 (± 1.3)	31.5	30.2 (± 1.6)	30.3	108.0	0.035
Fat score	2.9 (± 1.4)	2.5	2.8 (± 1.9)	2.8	182.0	0.856
Pectoral muscle	0.8 (± 0.3)	0.5	1.1 (± 0.6)	1.0	113.0	0.032
Body mass (g)	65.3 (± 9.8)	66.4	63.4 (± 8.6)	61.0	171.0	0.626

Table 4. Behavioural data of scan sampling analysed by means of ANCOVA (n = 206). Time of season was used as covariate (C). Significance was tested using bootstrap. 95% lower (L1) and upper (L2) confidence limits of the intercepts are listed (P < 0.05). * P < 0.05, *** P < 0.001.

| | Foraging | | Resting | | Scanning | | Fighting | |
	L1	L2	L1	L2	L1	L2	L1	L2
Season (C)	2.57	3.20 ***	−0.09	0.35	−0.04	0.17	−0.03	0.20
Age	18.06	30.22 ***	−3.44	8.63	1.91	5.73 ***	−0.44	2.06
Day-Slope 1	−0.27	6.66	−5.08	0.58	−1.41	0.96	−1.19	1.15
Day-Slope 2	−7.27	−0.53 *	−1.79	4.59	−1.01	1.53	−1.34	0.64
Age x Day-Slope 1	−3.18	4.22	−5.05	0.99	−1.87	0.42	−1.26	1.12
Age x Day-Slope 2	−2.22	6.02	−2.96	4.15	0.14	2.55 *	−0.43	1.82

$r^2 = 0.06$, P = 1.0, n = 13, juveniles: $y = -0.31x + 6.12$, $r^2 = 0.01$, P = 0.7, n = 18).

4.4. Behaviour

Our focal sampling data of individually-marked birds showed no correlation between fat score at first capture and the proportion of time spent foraging (adults: $y = -0.06x + 4.91$, $r^2 = 0.20$, P > 0.05, n = 11, juveniles: $y = -0.02x + 2.46$, $r^2 = 0.01$, P > 0.05, n = 56). The scan sampling data produced significant differences between age classes (Table 4): while juveniles were spending more time foraging, adults invested more time in surveillance (Fig. 3).

4.5. Fat load and flight range

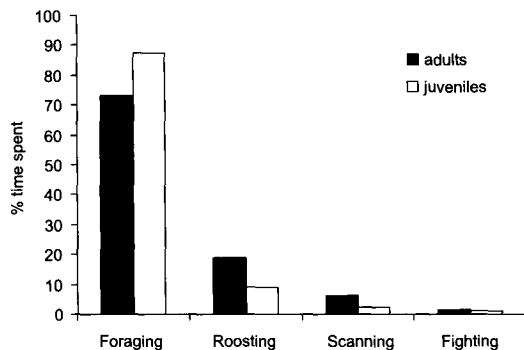Adults and juveniles differed significantly in fat score and body mass, adults possessing higher es-

Fig. 3. Time spent on different behavioural activities at Hohenau during Wood Sandpipers' autumn migration.

timated fat loads than juveniles. The fat load for the heaviest 10% of birds was 88% of the lean mass of adults (range: 70–96), and 67% of the lean mass in juveniles (range: 52–74), showing that the heaviest adults have almost doubled their body mass during migration – an average lean mass of 43.5 g was calculated for these birds (range: 41.7–48.2). The heaviest 10% of adults would be able to cover an average distance of 4178 km (range: 3419–4499), but the potential flight range in juveniles was an average of just 3368 km (range: 2668–3651). For the sake of comparison, the northern limit of the main wintering quarters is about 4,000 km away.

5. Discussion

5.1. Wood Sandpiper migration through Central Europe

The knowledge of the migration routes and dynamics of the Wood Sandpiper is fragmentary, particularly in Central and Eastern Europe (Remisiewicz 2002). Recoveries of Polish-ringed Wood Sandpipers in eastern Austria, western Hungary and the Czech Republic (Remisiewicz 1998, Laber 2003, Cepàk et al. 2003) suggest that the birds passing through this part of Central Europe are travelling across Poland in a south to south-south-west direction (Glutz v. Blotzheim et al. 1986, Scebba & Moschetti 1996, Meissner 1997, Holmgren & Pettersson 1998, Remisiewicz 1998 & 2002). They are then heading over the Alps to the west or the south, shown by recoveries in Italy and France of Wood Sandpipers ringed in Austria (Table 5), and may then be wintering anywhere in

Table 5. Within-year recoveries of Wood Sandpipers ringed or recovered in Austria (BirdLife Österreich Archives).

Ringing Site	Date	Recovery Site	Date	km
Walddorf, Carinthia, Austria 46°40'N, 14°20'E	14.08.1972	Bando, Ferrara, Italy	27.08.1972	295
Walddorf, Carinthia, Austria 46°40'N, 14°20'E	14.08.1972	Mirandola, Modena, Italy	27.08.1972	320
St. Peter a. Hart, Upper Austria 48°16'N, 13°06'E	16.08.1969	Gimeaux, Bouches-du-Rhône, France 43°39'N, 04°35'E	07.09.1969	833
Neusiedl a. See, Burgenland, Austria 47°57'N, 16°51'E	31.07.1964	Vauvert, Gard, France 43°41'N, 04°16'E	10.08.1964	1,083
Musov, Breclav, Czech Rep. 50°33'N, 13°11'E	29.07.1994	St. Anton a. d. Jesnitz, Lower Austria 47°57'N, 15°10'E	10.08.1994	147

western and southern Africa (e.g. Holmgren & Pettersson 1998, Stawarczyk 1998, Oschadleus 2002). Wood Sandpipers migrating through Central Europe apparently breed in Fennoscandinavia (Meissner 1997, Stawarczyk 1998, Remisiewicz 2002, Laber 2003). One Wood Sandpiper that had been ringed in southwest Finland was subsequently recaptured at Hohenau, fitting neatly into this picture. There is also evidence that Wood Sandpipers from Western Russia use the same migration route (Viskne & Mihelson 1985).

Table 2 clearly demonstrates that Wood Sandpipers caught at Hohenau are heavier than birds caught on the shores of the Baltic (Meissner 1997) or in Central Poland (Mitrus et al. 1998). Wood Sandpipers caught at a similar latitude to Hohenau – for example in Cholgynii in western Ukraine – show fairly similar body masses (Szydlowski & Lysaczuk 1998). Although trapping methods used at Ägelsee in Switzerland (Leuzinger & Jenni 1993) and the Volturno plain in Italy (Scebba & Moschetti 1996) differ from the other sites mentioned above, the differences in body mass to sites further north are still clearly visible. Consequently the birds appear to deposit fat continually as they travel south. Meissner (1997) states that juvenile Wood Sandpipers caught at Gdansk show a quick turnover and that the majority seem to travel short distances with low fat reserves, thus requiring a large number of feeding sites. In contrast, at inland stopover sites Wood Sandpipers show a lower turnover rate (Leuzinger & Jenni 1993, Wlodarczyk & Kaczmarek pers. comm., this study), which may be related to their preference for freshwater habitats (Glutz v. Blotzheim et al. 1986).

Some authors suggest that Wood Sandpipers use few stopover sites (OAG Münster 1988, Persson 1998, Anthes et al. 2002), but taking ringing recoveries into account, most of the birds either prefer short steps (Leuzinger & Jenni 1993, Persson 1998, Anthes et al. 2002) or are unable to carry out long-distance flights (Meissner 1997, Mitrus et al. 1998). An alternative explanation might be that migration strategies differ between the East Atlantic Flyway (cf. Anthes et al. 2002), running through Western Europe, and the Mediterranean Flyway, using inland stopovers in Eastern and Central Europe (cf. Remisiewicz 2002). We should also take into consideration the fact that due to human activities such as intensive land-use and riverbank stabilization, the number and the quality of stopover sites in Western Europe has decreased in comparison with eastern parts of Europe, so that the lack of suitable staging posts may force the birds using the East Atlantic Flyway into carrying out longer flights (cf. Leuzinger & Jenni 1993, Anthes et al. 2002).

5.2. Energy-selected or time-selected migration?

Meissner (1997) stated that most Wood Sandpipers migrating through the Gulf of Gdansk in autumn behave like energy-minimising migrants, but a small proportion of birds seem to maximise their speed instead: time-minimising migrants. He suggests that Wood Sandpipers alter their migration strategies in the face of unsuitable conditions such as bad weather. Looking at our data we can draw

similar conclusions. Time-selected migrants use fewer stopover sites and therefore should arrive in a fat-depleted condition. They should then try to accumulate fat as rapidly as possible, to be able to leave the area as quickly as possible. Time-selected migrants should therefore show a negative relationship between the length of stay and their fat load at ringing (Alerstam & Lindström 1990, Lyons & Haig 1995). As this correlation is absent from our data, Wood Sandpipers at Hohenau behave like energy-selected migrants. There was also no difference in fat load between transients and temporary residents: another indicator of energy-selected migration, for in time-selected migration the stopover decision is dependant upon both the actual fat load of the bird and the fat deposition rate (Alerstam & Lindström 1990). Unfortunately we have almost no data on fat accumulation. On the other hand, adults showed a higher level of fat loading than juveniles at Hohenau, which should be typical of time-selected migrants (Alerstam & Lindström 1990).

5.3. Adults versus juveniles

Increasingly greater differences occur between the body masses of adults and juveniles at staging areas further and further to the south (Tab. 2, Anthes et al. 2002). These differences could be attributed to the greater experience of the adults. One advantage of experience is an ability to increase the capacity for efficient foraging techniques (Burger 1988, Alerstam & Lindström 1990, Wunderle 1991), so adults could need fewer stopover sites. A higher proportion of transient adults is understandable from this view. Another explanation for both the differences in fat loading and the number of transient adults might simply be a better knowledge of suitable staging sites, as has been shown in Dunlins Calidris alpina by Dierschke (1998). We must also consider that experience in adults could influence their behaviour after capture, lowering the number of re-sightings.

Wood Sandpipers cross the Mediterranean and the Sahara to reach their wintering quarters, and it has been suggested that they may do this in one flight (Cramp & Simmons 1983, Yosef et al. 2002). According to our calculations, only the heaviest of the adults are capable of reaching the

northern limits of their African winter quarters. The amount of adults able to cover such a distance non-stop will of course increase as birds add to their fat deposits, but the vast majority of the birds still need additional refuelling sites. The difference between the distance that juveniles must still cover to reach their wintering grounds, and their potential flight range is somewhat more striking. Additional stopover sites are therefore even more essential for juveniles. It should of course be noted that any estimates of flight range should be treated with some caution, due to their various sources of error (Weber & Houston 1997). The birds' need for extra stopover sites in the Mediterranean is backed up by the fact that the majority of recoveries of birds ringed at Ägelsee in Switzerland (Leuzinger & Jenni 1993) and in Austria are short-distance (Table 5).

Both adults and juveniles spend most of their time feeding, in order to increase their potential flight range, but either due to their higher fat load or because of their more efficient foraging techniques, adults can afford to spend less time foraging. They can spend more time either alert for predators or resting, and are consequently at lower risk from predators. In a similar way, juvenile Dunlins are found to experience a higher predation rate than adults (Bijlsmar 1990, Dierschke 1998). Predation in general has a major impact on the survival of migrating birds and accordingly on migration strategies (Moore 1994, Lank et al. 2003, Lindström 2003).

Time of season proved to have significant influence on fat score for both age classes, in that birds arriving later in the season had more fat. Birds increased the amount of time spent foraging, and juveniles tended to shorten their length of stay at the site as the season progressed, suggesting a reaction to time running short. A higher fat score and a tendency to reduce the length of stay may be an insurance against any deterioration of food supply as the available time for migration runs short (e.g. Wilson 1988, Davidson & Morrison 1988).

5.4. Transients versus temporary residents

We found no biometric differences between temporary resident and transient adults. Transient juveniles showed shorter bills than temporary resi-

dents, which may be due either to different populations migrating through Hohenau or to sexual dimorphism. As we found no difference in wing length, transient juveniles should not be smaller-sized birds than temporary residents. However, transient juveniles may be those that try to avoid competition at small staging sites or that fail to compete effectively (Townshend 1985), an idea supported by a negligible number of fighting individuals (Fig. 3). Transients might use a different migration strategy to temporary residents, and by having better pronounced pectoral muscles may be able to migrate in longer stages, as pectoral muscle can be used both as an energy supply and to maintain optimal flight performance (Ramenowsky 1990, Lindström *et al.* 2000).

In conclusion, many of the Wood Sandpipers migrating through Central Europe in autumn have gained a substantial fat load by the time they reach north-east Austria. The birds appear to be moving in small stages through Central Europe, with short stops at a large number of sites. According to our flight-range estimates, Wood Sandpipers must use additional staging areas around the Mediterranean to be able to cross the barriers of the Mediterranean Sea and the Sahara. We found strong evidence that juveniles are more vulnerable to time and energy shortages during migration. As juvenile birds carry lower fat loads than adults, they necessarily expend greater effort in foraging to maintain sufficient fat loads to cross these barriers. In turn, the more time is spent on foraging, the less is available for surveillance and so juveniles are more vulnerable to predation. They also seem to be more vulnerable to competition, as a proportion of the migrating juveniles are adapted to migrate further on.

Ikään liittyvät liron muuttoaikaiset levähdysstrategiat

Artikkelin kirjoittajat pyydystivät ja rengastivat syysmuuton aikana liroja Itävallan Hohenaun alueella vuosina 2000–2003. Aineisto koostui 80 aikuisesta ja 66 nuoresta lirosta, joista 38 aikuista ja 36 nuorta lintua oli merkitty yksilöllisesti. Lirot keräävät vähitellen rasvavarastoja pitkin muuttomatkaansa. Hohenaussa lirojen rasvaindeksi kasvoi muuttokauden edessä. Korkea rasvan määrä muuttokauden loppupuolella voi kompensoida mahdollisesti huonontuvaa ravintotilannetta. Aikuiset lirot olivat painavampia ja niillä oli enemmän rasvaa kuin nuorilla liroilla. Nuoret lirot joutuvat käyttämään enemmän aikaa ruokailuun kerätäkseen rasvavarastoja ja näin ollen ne ovat aikuisia lintuja herkempiä ravinto-olojen heikkenemiselle ja predaatiolle.

Tutkimuksessa ei nuorten lintujen välillä havaittu kilpailua. Ohikulkumatkalla olevat nuoret lirot (yksilöt, joita ei havaittu paikalla rengastuksen jälkeen) voivat olla sopeutuneita muuttamaan pidempiä välimatkoja kuin hetkellisesti paikalliset lirot (yksilöt, jotka viipyivät rengastuspaikalla vähintään yhden päivän). Tulosten mukaan muuttoaikainen ravintopula ja ajanpuute vaikuttavat enemmän nuoriin liroihin kuin aikuisiin liroihin. Useimmat lirot, erityisesti nuoret yksilöt, näyttävät tarvitsevan runsaasti levähdysalueita kerätäkseen Välimeren ja Saharan ylitykseen tarvittavan rasvavaraston.

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