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The autumn migration of Willow Warblers *Phylloscopus trochilus* in Sweden: results from a nation-wide co-operative project

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Abstract

The result of a nation-wide co-operative project studying the autumn migration of Willow Warblers *Phylloscopus trochilus* in Sweden is presented. This involved 18 bird observatories and private ringers during 1988–1990, at both coastal and inland sites, with data on more than 36 000 birds analysed. Data on age, wing length, fat and body mass were collected in a standardised way, as was scoring of post-juvenile moult (used as a measure of juvenile age). Each bird observatory made a basic compilation of data into weekly averages, upon which the present analysis builds. The proportion of juveniles (93%) was much higher than expected (c.75%), at both inland and coastal sites. Adults migrated a few days later than juveniles. There was no sex difference in the timing of migration in adults. Juveniles of *Ph.t.acredula* started migration at an earlier age (35–40 days old) than juveniles of *Ph.t.trochilus* (50–55 days old). Average wing length increased during the season at many sites, suggesting that birds belonging to the longer-winged *Ph.t.acredula* passed later in season. Juvenile energy stores were small during mid post-juvenile moult, but higher in the last moult stage, especially at coastal sites. Generally, Willow Warblers in Sweden in autumn carry only small to moderate fat loads, which supports earlier findings that the commencement of migration involves short flights. Conclusions on energy stores were based on data from visual fat score. Because both moulting and migrating birds occurred at most sites, and moulting birds have a different composition of their lean body, body mass does not reflect the seasonal changes in fat loads. Body mass averages of 8.2–9.3 g were similar to averages from other parts of northern Europe, but below the values reported for birds prior to trans-Sahara flights and maximum masses of birds in captivity.

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Introduction

Many birds cover vast distances between their winter and summer quarters. An endogenous program ensures that they migrate within an appropriate time period and on a relevant course (Gwinner 1996). The migrants are likely to encounter different environmental conditions such as weather, stopover habitat quality and predators, which will affect their migratory performance (e.g. Alerstam 1982, Alerstam & Lindström 1990). Conclusions about the migration ecology of a population or a species have previously often been drawn from studies at only one or a few stopover sites. For a better understanding of the performance of migratory birds, and the selection pressures operating on them, it is necessary to study them at as many sites as possible along the migratory route. The nation-wide co-operative study of the autumn migration of Willow Warblers *Phylloscopus trochilus* in Sweden, reported in this paper, is an attempt at this.

Two subspecies breed in Sweden (Salomonsen 1945, SOF 1990): the nominate subspecies *Ph.t.trochilus* in the southern third (or half) of Sweden, which migrates south-west in the autumn to winter quarters in sub-Saharan West Africa, and the somewhat larger *Ph.t.acredula* (Salomonsen 1945, Fonstad & Hogstad 1981), which breeds in northern Sweden and migrates south-south-east to wintering grounds in Central, East and South Africa (Hedenström & Pettersson 1987). During autumn, migration over south-western Sweden mainly involves *trochilus* birds, whereas both subspecies occur in south-eastern Sweden, with the northern population passing somewhat later in the season (Hedenström

& Pettersson 1984, 1987, Pettersson & Hedenström 1986).

This paper analyses the age proportion, timing, wing length, fat score, body mass and extent of post-juvenile moult in relation to autumn migration of Willow Warblers moving through Sweden. The occurrence of interrupted secondary moult in autumn migrating adults, based on results from the same project, was presented by Hedenström et al. (1995).

Methods

"Project Willow Warbler"

The project was initiated in December 1987 at a meeting with representatives for Swedish bird observatories. The aims were threefold: 1) to gather a large data set about the performance of a species migrating through Sweden, 2) to promote goal-directed data gathering and analysis among bird observatories and ringers, and 3) to strengthen co-operation between bird observatories (Hedenström et al. 1989).

The Willow Warbler is one of a few species caught in large numbers at most bird observatories and by ringing groups and private ringers. The potential was there to include many ringing sites from around the country. Studies on the Willow Warbler have been carried out in both Sweden (e.g. Högstedt & Persson 1982, Hedenström & Pettersson 1984, 1986, 1987, Betzholtz 1988, 1989) and Great Britain (e.g. Baggott 1975, 1986, Norman 1981, 1983, 1987, Lawn 1984, Norman & Norman 1985), which the results could be related to.

An important aim of the project was to promote bird observatories and ringers to collect data in a standardised way, and analyse these to a certain degree themselves. As project leaders we took responsibility for co-ordinating these efforts, and to undertake the final analyses of the overall data set.

The participants were asked to make a preliminary analysis of their data on standardised forms. This had at least three important effects on the outcome of the project. First, several observatories showed interest but never submitted any data, or for only one or two years, even if data had been collected. Second, the whole analysis is based mainly on average values from the different sites, which restricted the type of analyses that could be made. Third, during the analysis it became clear that the way in which the data was reported was not always optimal, and in some cases interesting analyses were not possible to carry out.

Data collection

The participants made a habitat description of their catching area, and reported the number of nets used, the number of days of trapping, and the first and last day of catching each season (Appendix 1). Birds were aged as juveniles (first-calendar year, Euring-code 3) or adults (second-calendar year or older, Euring-code 4), following Svensson (1984). Wing length was measured to the nearest mm (method 3, Svensson 1984). The amount of visible fat was scored on a scale from 0 to 6 (Pettersson & Hasselquist 1985), where 0 denotes no visible fat, and 6 large fat stores (for the relationship between this scale and true fat stores in Willow Warblers, see Lundgren et al. 1995). Fat score was not sampled in 1988. Birds were weighed to the nearest 0.1 g. Only fat scores and body masses of birds caught before 12.00 (noon, local time) were reported.

A scale from 1 to 6 was used to estimate the extent of post-juvenile moult on the ventral tract in juvenile birds (Bensch & Lindström 1992). The different moult stages correspond to a certain average age: stage 1 = 21 days, 2 = 27 days, 3 = 32 days, 4 = 37 days and 5 = 44 days (Bensch & Lindström 1992). No estimate for stage 6 was made, but birds that have finished moult are older than 60 days (Gwinner 1969, Norman 1981). The study of Bensch & Lindström (1992) concerned the northern subspecies *acredula*. It is unknown how the scale compare to the southern subspecies *trochilus*, but as similarities were found between this scale and that of British *trochilus* birds (Norman 1981), it is likely that the scale is also representative for Swedish *trochilus*.

Birds retrapped one day or more after first capture were processed in the same manner as when first handled.

Data analysis

Most data were compiled into weekly averages by the participants (including standard deviation and sample size), with each week denoted by the standard calendar week number. Data were reported for weeks 29–39, encompassing the complete autumn migration period and corresponding to the following annual dates: 18 July – 2 October 1988, 17 July – 1 October 1989, and 16 July – 30 September 1990. For sake of clarity, when presenting data relating to different week numbers, we present a date corresponding to the Thursday of each week.

Median catching dates for adults and juveniles, respectively, were calculated by each project partic-

Fig. 1. Location of the 18 participating ringing sites and median trapping dates of adults and juvenile Willow Warblers in the autumns of 1988, 1989 and 1990. Median dates are presented only for sites where at least 30 juveniles and adults were caught. Geographical co-ordinates are given in Table 1.

Karta över de 18 deltagande ringmärkningsstationerna samt mediandatum för fångst av gamla respektive unga lövsångare hösterna 1988, 1989 och 1990. Mediandatum presenteras endast för lokaler där minst 30 av respektive åldersgrupp fångats. Geografiska koordinater presenteras i Tabell 1.

Site	Age	1988	1989	1990
1	Ad	26 Jul	27 Jul	25 Jul
	Juv	8 Aug	6 Aug	2 Aug
2	Ad		28 Aug	13 Aug
	Juv	18 Aug	17 Aug	20 Aug
3	Ad		19 Jul	25 Jul
	Juv		29 Jul	2 Aug
4	Ad	28 Aug		4 Sep
	Juv	28 Aug		2 Sep
5	Ad			11 Aug
	Juv		27 Aug	10 Aug
6	Ad			
	Juv	13 Aug	11 Aug	7 Aug
7	Ad			
	Juv	6 Aug	19 Aug	8 Aug
8	Ad	28 Aug		
	Juv	28 Aug		
9	Ad			
	Juv	6 Sep	29 Aug	5 Sep
10	Ad	8 Aug		
	Juv	5 Aug	24 Aug	10 Aug
11	Ad			
	Juv	11 Aug	21 Aug	5 Aug
12	Ad	27 Aug		
	Juv	23 Aug		
13	Ad			
	Juv	24 Aug	14 Aug	18 Aug
14	Ad	23 Aug	3 Sep	4 Sep
	Juv	21 Aug	20 Aug	16 Aug
15	Ad			
	Juv			
16	Ad	31 Aug		7 Sep
	Juv	28 Aug	30 Aug	2 Sep
17	Ad			
	Juv		16 Aug	13 Aug
18	Ad	26 Aug		
	Juv	23 Aug	16 Aug	15 Aug

ipant. The proportion of birds retrapped was also reported, as was the proportion of birds which increased more than 2 fat classes, or more than 1.0 g in mass, since ringing.

In order to investigate sex-specific differences in migration performance, birds were divided into males and females according to wing length (Norman 1983, Svensson 1984). The following wing length criteria were used: adult male ≥69 mm, adult female ≤66 mm, juvenile males ≥68 mm, and juvenile females ≤65 mm. Birds of the *acredula* subspecies have somewhat longer wings than the *trochilus* birds (approximately 1 mm, Fonstad & Hogstad 1981, Hedenström & Pettersson 1984). The chosen wing length criteria will therefore include different proportions of the two sexes for each of the subspecies. This problem is difficult to overcome, since the subspecies cannot be separated on plumage characteristics in autumn. Also, the averages assigned to males and females, are not completely representative values for the sexes: "males" include all males apart from the smallest ones (shortest wings) and "females" include all females apart from the largest ones (longest wings). For example, for body mass the difference between the averages for the two sexes becomes exaggerated due to the wing-length interval classification.

Sample size varied greatly between sites and years, and for the different types of information gathered. We decided to include data points only if based on at least 30 birds. When looking at seasonal trends within one site we only included sites where a

Table 1. Number of adult and juvenile Willow Warblers caught during the autumns of 1988–1990 by the participating observatories and ringers. The percentages of juveniles are also shown. Each ringing site was classified as either inland (I) or coastal (C). The location of each site is shown in Fig. 1.

Antalet adulta och juvenila lövsångare fångade under höstarna 1988–1990 vid de olika fångststationerna. Andelen (i procent) ungfåglar redovisas också. Varje lokal klassades som antingen inlandslokal (I) eller kustlokal (C). De olika platsernas geografiska läge visas i Fig. 1.

			1988			1989			
	Locality *Plats*	I/C	Ad	Juv	Juv %	Ad	Juv	Juv %	Ad
1	Ammarnäs	I	43	677	94	82	759	90	39
2	Haparanda S	C	29	1117	97	59	1823	97	215
3	Ånnsjön	I	93	805	90	404	817	67	238
4	Eggegrund	C	68	619	90	–	–	–	106
5	Idö, Mälaren	I	24	340	93	28	133	83	44
6	Ässön	I	18	354	95	9	260	97	10
7	Kvismaren	I	25	348	93	5	167	97	23
8	Stegsholm	C	55	564	91	–	–	–	–
9	Landsort	C	7	527	99	21	659	97	28
10	Hornborgasjön	I	32	843	96	15	247	94	26
11	Landsjön	I	12	625	98	5	231	98	6
12	Nidingen	C	226	848	79	–	–	–	–
13	Oskarshamn	I	12	138	92	4	105	96	13
14	Sundre	C	78	2875	97	68	1476	96	73
15	Kalmar	C	–	–	–	1	26	96	–
16	Ottenby	C	35	898	96	26	825	97	49
17	Jordberga	I	–	–	–	5	78	94	5
18	Falsterbo	C	153	2026	93	69	964	93	18
	Total *Summa*		910	13604	94	801	8570	91	893

minimum of 30 birds were trapped per week for a minimum of six weeks. These selection criteria have by necessity drastically reduced the number of data points included in the analyses and hence the power of our conclusions. However, we preferred this to the risk of discussing effects due to the unavoidable random scatter of small samples.

Statistics

Statistical tests were conducted using SYSTAT (Wilkinson 1990). All tests were parametric, apart from Spearman rank correlations used to test within-seasonal trends. All significance tests were two-tailed. For ANOVAs and ANCOVAs non-significant interaction-terms were excluded. Tests for normality were done on the residuals from ANOVAs, ANCOVAs and regressions with the Lilliefors test. If residuals were not normally distributed, the original data were log-transformed. Proportions were transformed using square root and arcsin-transformation to obtain normal distributions, but in presentations the original values have been used. Most of the statistical tests are listed in Appendix 2 and only referred to as T1, T2 etc. in the text.

Results

Participating ringing sites

A total of 18 bird observatories, ringing groups or private ringers sent in data for at least one of the three seasons (Table 1, Fig. 1). More than 36,000 birds were trapped. However, for various reasons, not all the data asked for was recorded on all birds, or were not compiled or reported.

The sites are widely distributed over Sweden, with the distance between the northernmost and southernmost site (Ammarnäs and Falsterbo) being approximately 1200 km. However, most of the sites are situated in the southern third of Sweden, which reflects the distribution of ringing activities in the country.

Habitat description: Sites 1 and 3 are situated within the Scandinavian mountain range, and field work was undertaken in river- and lakeside habitats dominated by birch and willows. Sites 2, 4, 9 and 12 are located on small coastal islands several kilometres from the mainland. Sites 5, 6, 7, 10, 11 and 17 are lakeside ringing sites (site 17 is in an area of artificial ponds), mainly dominated by reed beds, but also

1990		1988–1990			
Juv	Juv %	Ad	Juv	Juv %	Total *Summa*
565	94	164	2001	92	2165
1822	89	303	4762	94	5065
1388	85	735	3010	80	3745
1170	92	174	1789	91	1963
205	82	96	678	88	774
404	98	37	1018	96	1055
280	92	53	795	94	848
–	–	55	564	91	619
697	96	56	1883	97	1939
562	96	73	1652	96	1725
423	99	23	1279	98	1302
–	–	226	848	79	1074
322	96	29	565	95	594
1486	95	219	5837	96	6056
–	–	1	26	96	27
1385	97	110	3108	97	3218
177	97	10	255	96	265
447	96	240	3437	93	3677
11333	93	2604	33507	93	36111

includes bushes and low forest. Site 8 and 15 border the sea, with both reed beds and shrubberies within the catching area. Site 13 is located at a sparsely vegetated old rubbish dump, including a few bushes and trees. Finally, sites 14, 16 and 18 are at the outermost tips of peninsulas bordering the Baltic Sea.

The sites were classified as either inland or coastal (Table 1), based on both geographical and "migrational" criteria. The coastal sites are all close to the sea shore, normally rather exposed places on islands and tips of peninsulas. The inland sites are at least 20 km from the sea, the one exception being the site outside Oskarshamn (site 13), which is only 1 km from the sea, but migrants occur there independent of daily weather changes (T. Larsson, pers. comm.), the opposite to typical coastal sites. Site 13 was therefore considered an inland site.

Trapping effort: Time periods and number of days of ringing are shown in Appendix 1. Most sites covered the main migration period, even though catching was only carried out a few days per week at some places. The number of nets (and net hours) varied considerably between sites (not presented) which would influence the number of birds caught. However, since the analyses are mainly concerned with between-site comparisons of averages, the influence of trapping effort on the results and their interpretation will be minor.

Age proportions

The proportion of juveniles each year varied from 67% to 99% between sites and years (Table 1). Juvenile proportions below 90% were reported from Ånnsjön (site 3), Idö (5) and Nidingen (12). For the 13 localities where data were available for all three years, there were no significant differences between years (T1). We therefore used the overall proportions (1988–1990, see Table 1), and included all 18 sites, for further analyses. Age proportions were not significantly correlated with either latitude or locality (inland/coastal) type (T2).

Seasonal trends within sites: In total, 25 year-values from 13 sites could be used (6–9 weeks per year and site) for analysis. The general trend showed the proportion of juveniles decreased over the course of the autumn (19 out of 25 Spearman rank correlations showed a negative slope, although only two of them were significant (site 14: $P<0.01$ in both 1989 and 1990). However, the absolute values normally varied to a very limited extent.

Timing of migration

The median dates for adults and juveniles each year are shown in Fig. 1.

Latitude and locality type: Among adults, latitude had a significant negative effect on trapping date in one year, whereas locality type had a significant influence all three years (T3). Adults were on average caught 26, 36, and 31 days earlier, respectively, at inland localities than at coastal localities in the three study years. Among juveniles, latitude had no significant effect on trapping date, whereas locality type had a significant effect in two years (T4). Juveniles were on average caught 15, 7, and 17 days earlier at inland localities than at coastal localities in the different years. This is also reflected in the differences in moult score between inland and coastal localities (see below).

Median dates from inland sites were not representative for timing of migration, since catches at inland sites include both moulting and migrating birds. However, at coastal sites, birds are probably

Table 2. Average wing lengths of adult and juvenile Willow Warblers during the autumns of 1988–1990. Data are only shown when more than 30 birds of an age group were caught within one season. The location of each site is shown in Fig. 1.

Medelvinglängd hos gamla och unga lövsångare höstarna 1988–1990. Medelvärden visas endast om minst 30 fåglar i en åldersgrupp fångats under säsongen. De olika platsernas geografiska läge presenteras i Fig. 1.

		1988		1989		1990	
	Locality *Plats*	Ad	Juv	Ad	Juv	Ad	Juv
1	Ammarnäs	68.2	67.1	68.3	67.5	67.0	67.1
2	Haparanda S	–	67.3	66.6	66.6	65.6	66.4
3	Ånnsjön	66.4	66.1	66.3	66.6	66.4	65.8
4	Eggegrund	67.4	66.8	–	–	67.8	67.7
5	Idö, Mälaren	–	–	–	67.5	67.4	66.7
6	Ässön	–	66.3	–	66.2	–	66.9
7	Kvismaren	–	66.4	–	66.1	–	66.6
8	Stegsholm	68.1	67.2	–	–	–	–
9	Landsort	–	66.4	–	66.0	–	66.9
10	Hornborgasjön	65.7	65.9	–	65.6	–	65.8
11	Landsjön	–	66.0	–	65.3	–	65.2
12	Nidingen	67.6	66.9	–	–	–	–
13	Oskarshamn	–	65.8	–	64.7	–	65.7
14	Sundre	66.8	66.4	67.8	66.0	67.2	65.8
16	Ottenby	68.8	66.2	–	66.0	66.8	66.0
17	Jordberga	–	–	–	66.4	–	66.2
18	Falsterbo	67.7	66.5	67.9	66.5	–	65.7

Table 3. Average moult score of juvenile Willow Warblers for each autumn 1988–1990, for week 32 (approximately 10 August) and week 34 (approximately 24 August). Only values based on a minimum of 30 birds are presented. The location of each site is shown in Fig. 1.

Medelruggstadium hos unga lövsångare höstarna 1988–1990, samt medelruggstadium veckorna 32 (c. 10 augusti) och 34 (c. 24 augusti). Endast medelvärden baserade på minst 30 fåglar presenteras. De olika platsernas geografiska läge presenteras i Fig. 1.

		Seasonal average *Medelvärde hösten*			Week 32 *Vecka 32*			Week 34 *Vecka 34*		
	Locality *Plats*	1988	1989	1990	1988	1989	1990	1988	1989	1990
1	Ammarnäs	2.8	2.4	2.4	3.2	2.6	3.1	4.2	–	–
2	Haparanda S	4.7	3.8	3.3	3.7	3.3	3.2	5.4	5.2	3.1
3	Ånnsjön	3.6	2.8	2.7	3.9	2.8	3.1	5.5	3.9	4.5
4	Eggegrund	5.8	–	5.8	–	–	–	5.9	–	5.7
6	Ässön	4.4	4.3	4.0	4.9	4.6	4.1	–	–	–
7	Kvismaren	4.1	4.5	4.1	4.9	–	4.5	4.2	–	–
8	Stegsholm	5.2	–	–	5.1	–	–	5.7	–	–
9	Landsort	5.5	5.4	5.5	–	–	4.3	5.6	5.2	5.4
10	Hornborgasjön	4.1	3.7	4.4	4.2	4.2	4.7	4.8	–	4.6
11	Landsjön	4.6	3.6	3.9	4.3	–	4.0	–	–	–
12	Nidingen	5.7	–	–	5.7	–	–	5.6	–	–
13	Oskarshamn	–	4.5	–	–	–	–	–	–	–
14	Sundre	4.5	4.6	4.7	3.9	4.1	4.6	5.1	5.1	5.3
16	Ottenby	5.5	5.1	5.3	5.3	4.7	4.5	5.6	5.4	5.1
17	Jordberga	–	4.7	5.0	–	–	–	–	–	5.6
18	Falsterbo	5.7	5.4	5.2	5.3	5.1	5.4	5.9	5.7	5.4

on migration. The effect of latitude on median dates was therefore analysed separately for coastal sites, but only for years with data from at least five sites. Among adults (only 1988 was analysed), there was no significant effect of latitude on median capture date (T5). This was also the case for juveniles in all three years (T6).

In conclusion, Willow Warblers were not caught significantly later in the season in southern than in northern Sweden, as may have been expected from their southerly migration direction. Locality type was very important, with inland localities catching Willow Warblers on average 2–4 weeks earlier than coastal sites.

Age differences: The difference in median trapping date between age groups did not vary between years (T7), but a strong effect of locality type was apparent (T8). At the two inland localities in Lapland, site 1 and 3, adults were caught between 8 and 13 days earlier than juveniles each year. In contrast, at the coastal localities, adults were normally trapped 0–5 days later than juveniles (with the exception of locality 2 in 1989, and locality 14 in 1989 and 1990, where adults were caught 11–19 days later than juveniles).

Sex differences: Overall there were no significant differences in median dates of trapping between adult males and adult females (T9). The differences at each site and year varied between 0 and 11 days. Moreover, the normally small differences between the sexes were not explained either by year or locality type (T10).

Wing lengths

Average wing lengths are shown in Table 2.

Effect of latitude: Among adults there was no effect of year on average wing lengths, and no significant correlation with latitude (T11). Among juveniles, year had no effect on average wing length, but there was a significant correlation between latitude and average wing length (T12). For each of the three years, the regression coefficient for juvenile wing length against latitude was positive and significant or close to significant (T13). Thus, juvenile Willow Warblers had on average longer wings the more northerly in Sweden they were trapped, but this did not occur in adults. At sites 1 and 3, but not at the other sites, almost all adults were trapped before post-nuptial moult. These birds have worn outer primaries and the wing-lengths recorded are relatively shorter than for birds that have just finished post-nuptial moult.

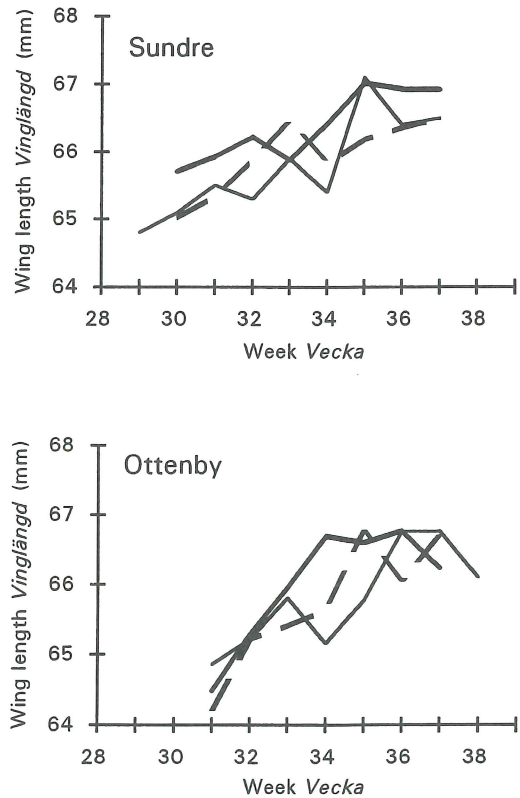


Fig. 2. Weekly average wing lengths (mm) of autumn migrating juvenile Willow Warblers at Ottenby (site 16) and Sundre (site 14). Data are shown for three years (1988: thick solid line, 1989: dashed line, 1990: thin solid line).

Medelvinglängd per vecka hos unga lövsångare på höstflyttning vid Ottenby och Sundre. Data för tre år presenteras (1988: fet heldragen linje, 1989: streckad linje, 1990: tunn heldragen linje).

Seasonal trends within a site: The longer-winged northern Willow Warblers are assumed to migrate over southern Sweden slightly later in autumn than *Ph.t.trochilus*, and on a south-easterly bearing (Hedenström & Pettersson 1984). We therefore looked at the seasonal trends of wing lengths at each site. Insufficient numbers of adult birds were measured to meet the minimum selection criterion. However, among juveniles, a total of 23 year-values from 11 sites (sites 2–3, 7–12, 14, 16 and 18) was available (6–9 weeks per year and site). There was a general trend that the weekly average wing length increased as the season progressed; 21 out of 23 Spearman correlation coefficients were positive. Eight of them were significant: site 10 in 1990 (p<0.01), site 18 in 1990 (p<0.05), and all three years at sites 14 and 16 (p<0.05 and p<0.01, see Fig. 2).

Age differences: Within each site, adults had on average longer wings than juveniles (Table 2), the differences being 0.84, 0.74 and 0.39 mm in the three study years (T14).

Post-juvenile moult

The moult stage of juvenile Willow Warblers at different sites and time periods are shown in Table 3.

Latitude and locality type: The overall seasonal averages were significantly correlated with both latitude and locality type (T15). Average moult scores were higher for birds caught in southern Sweden, and higher at coastal than inland localities. However, the fact that median dates of trapping differed between localities (see above), should also be reflected in average moult scores. Therefore only the average moult scores at different sites during two specific calendar periods were analysed.

During week 32 (approximately 10 August) average juvenile moult scores were significantly higher the further south the birds were caught, but there were no significant differences between inland and coastal localities (T16).

During week 34 (approximately 24 August) the situation was less clear. In only two years, 1988 and 1990, were data sets large enough for an analysis. In 1990, the pattern was similar to week 32 with the average juvenile moult score significantly higher the further south the birds were caught and with no differences between inland and coastal localities (T17). However, in 1988 there was no significant effect of latitude, whereas birds at inland localities had significantly lower mean moult scores than the birds at coastal localities (T18)

For those localities where data were available for all three years, tests were undertaken on differences between years in average moult scores. For seasonal average moult score, as well as average moult scores in week 32 and 34, the values were highest in 1988, but not significantly so (T19).

Fat scores

Average fat scores for adults and juveniles at the different sites in 1989 and 1990 are shown in Table 4. No significant difference was apparent in either age group for average fat scores between the years, based on sites with data available in both years (T20).

Table 4. Average fat scores of adult and juvenile Willow Warblers during the autumns of 1989–1990. Data are only presented when more than 30 birds of an age group were caught within one season. The location of each site is shown in Fig. 1.

Genomsnittliga fettvärden hos gamla och unga lövsångare höstarna 1989–1990. Medelvärden visas endast om minst 30 fåglar i en åldersgrupp fångats under säsongen. De olika platsernas geografiska läge presenteras i Fig. 1.

		1988		1989	
	Locality *Plats*	Ad	Juv	Ad	Juv
1	Ammarnäs	0.85	1.03	–	1.19
2	Haparanda S	1.73	1.65	2.24	2.29
3	Ånnsjön	1.36	1.43	0.85	1.01
4	Eggegrund	–	–	3.36	3.37
6	Ässön	–	1.11	–	0.93
7	Kvismaren	–	1.35	–	0.78
9	Landsort	–	3.23	–	3.44
10	Hornborgasjön	–	1.60	2.81	2.04
11	Landsjön	–	2.66	–	2.66
13	Oskarshamn	–	2.60	–	2.59
14	Sundre	2.97	2.86	3.58	2.26
16	Ottenby	–	3.04	4.00	3.28
17	Jordberga	–	1.81	–	1.68
18	Falsterbo	4.78	3.37	–	2.80

Age differences: Although too few adults were caught to compare in detail fat scores between age groups (Table 4), there was a trend for adults to have slightly higher fat loads than juveniles, especially at the southern coastal observatories.

Latitude and locality type: Among adults, there were no significant effects of either latitude or locality type on average fat scores in 1989 (T21). In 1990, there was a significant effect of both latitude and locality type (T22). However, due to the small number of sites included for adults, conclusions should be treated with caution. Among juveniles, latitude and locality type had a significant effect on fat score in one and two years, respectively (T23). Fat scores increased towards the south, and were higher at coastal than inland localities, in both years and both in adults and juveniles. However, since juvenile Willow Warblers were trapped in different moult stages (age) at the different sites (see above), average fat scores may be influenced also by the age of the birds. We therefore compared average fat scores for birds of similar moult score (age).

For the following analyses we used the average fat score for the first week at each site when an average moult score above 3.0 and 5.0 was recorded (Table

Table 5. Average fat scores of juvenile Willow Warblers in different moult stages (MS). The values are the average fat scores for the first week at each site when birds had reached an average moult score of at least 3.0 and 5.0. Data are only shown when more than 30 birds were caught in one week. The median day of the week from which the data are collected is also presented. The location of each site is shown in Fig. 1.

Genomsnittliga fettvärden hos unga lövsångare i olika stadier av kroppsruggning (MS). Värdena som presenteras är de genomsnittliga fettvärdena den första vecka som fåglarna i genomsnitt var i ruggningstadium 3.0 respektive 5.0. Medelvärden visas endast om minst 30 fåglar fångats på en vecka. Datumen motsvarar torsdagen i den vecka från vilken värdena är hämtade. De olika platsernas geografiska läge presenteras i Fig. 1.

		1989				1990			
	Locality *Plats*	MS > 3		MS > 5		MS > 3		MS > 5	
1	Ammarnäs	0.9	17 Aug	–	–	1.0	9 Aug	–	–
2	Haparanda S	0.5	10 Aug	3.0	24 Aug	0.5	9 Aug	–	–
3	Ånnsjön	1.1	17 Aug	–	–	1.4	9 Aug	–	–
4	Eggegrund	–	–	–	–	–	–	3.0	16 Aug
6	Ässön	0.4	20 Jul	1.9	31 Aug	0.4	26 Jul	–	–
7	Kvismaren	0.6	27 Jul	1.5	31 Aug	0.7	26 Jul	–	–
9	Landsort	–	–	3.2	17 Aug	–	–	3.6	16 Aug
10	Hornborgasjön	1.3	20 Jul	–	–	1.3	19 Jul	2.5	30 Aug
11	Landsjön	–	–	–	–	2.1	26 Jul	–	–
14	Sundre	1.6	27 Jul	3.2	24 Aug	0.4	26 Jul	3.4	23 Aug
16	Ottenby	–	–	3.0	17 Aug	–	–	3.1	23 Aug
18	Falsterbo	0.1	20 Jul	3.3	10 Aug	0.8	26 Jul	3.7	9 Aug

5). This was done because many juveniles with moult scores of around 3 (about 32 days old) may not have commenced true migration, whereas at an average moult score of 5 (about 44 days old), many or most of the birds have set out on migration (Norman 1994). Due to the way data were reported we were unable to analyse fat scores of individual birds at different moult scores.

Among juvenile Willow Warblers with an average moult score of 3, fat score was neither correlated to latitude nor locality type (T24, Table 5, Fig. 4). During moult score 5 in 1989, fat score was not related to latitude, but fat scores were significantly higher (3.1 vs. 1.7) at coastal sites (T25). In 1990, only one inland site had sufficient data, therefore only the effect of latitude could be investigated, but no effect was found (T26).

At the few sites where sufficient birds were caught in both moult stages in one year, the fat scores in the two moult stages were compared. Birds in moult score 5 had significantly higher fat scores than those in moult stage 3 (T27).

This suggests juvenile Willow Warblers in moult stage 3 have the same low fat loads (range 0.1–1.6) throughout Sweden. Older juveniles (moult score 5) at coastal sites have probably already commenced migration and show higher fat scores (range 2.9–3.7) than those of a similar age at inland sites (range 1.5–2.5). At any site, fat scores were higher in older juveniles (on average the fat score was 0.9–3.2 classes higher), the difference being higher at coastal sites.

Seasonal trends within sites: In total, 11 year-values from 7 sites could be used. There was a general trend that the fat scores of juveniles increased with time of season (10 out of 11 Spearman rank correlations were positive, four of them being significant (site 2, 3 and 14, $p < 0.01$; site 10, $p < 0.05$, all in 1990, Fig. 5). Too few adults were caught to permit a similar analysis.

Proportion of obese birds: To analyse the occurrence of obese birds among migrants only birds on active migration were used. Therefore only birds trapped in the latter part of the autumn, starting with the week when the average juvenile moult score at each site was at least 5.0 were included. Since no corresponding criteria were available for adults, we used the same time period as for juveniles at each particular site. Few birds with fat score 6 were trapped (Table 6) and combining all sites, the figure for adults was only 8.5% (16 out of 188 birds) in 1989 and 2.4% (6/254) in 1990. The corresponding figures for juveniles were 3.0% (95/3117) in 1989 and 2.6% (98/3797) in 1990. At those sites where at least 30 birds of an age group were processed in one year, the highest proportions of fat birds were found

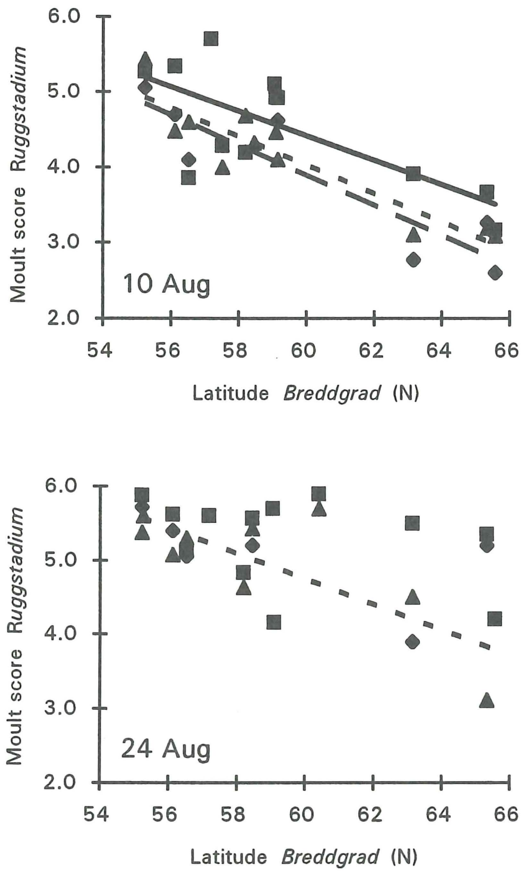


Fig. 3. Average juvenile moult scores in week 32 (approximately 10 August) and week 34 (approximately 24 August) in relation to latitude of ringing. Data are shown separately for the three study years (1988: ■, solid line; 1989: ◆, dashed line; 1990: ▲, dotted line). Lines are only presented for significant relationships between latitude and moult score. All data points include at least 30 birds caught each week.

Medelruggstadium under vecka 32 (ungefär 10 augusti) och vecka 34 (ungefär 24 augusti) i förhållande till märkplatsens breddgrad. Data från de tre studieåren presenteras var för sig (1988: ■, heldragen linje; 1989: ◆, streckad linje; 1990: ▲, prickad linje). Linjer visas bara i de fall där det råder ett signifikant samband mellan breddgrad och ruggstadium. Värden presenteras bara för de platser och år där minst 30 fåglar fångats under vecka 32 respektive 34.

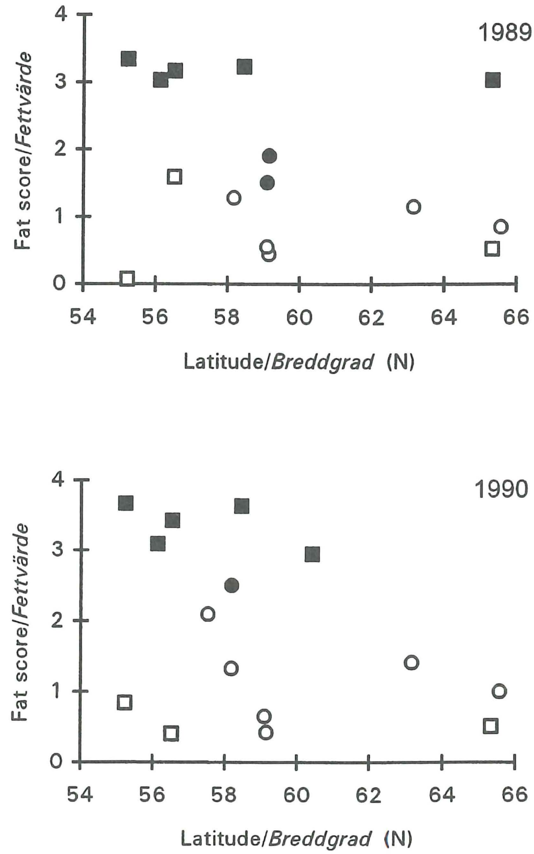
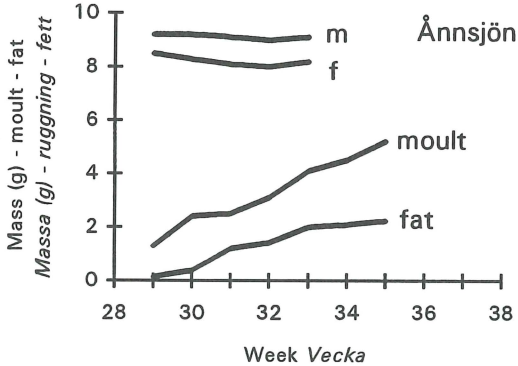


Fig. 4. Average fat scores of juvenile Willow Warblers in relation to latitude and locality type in the first week the average moult stage reached at least 3 and 5, respectively (□ = moult stage 3, coastal site; ○ = moult stage 3, inland site; ■ = moult stage 5, coastal site; ● = moult stage 5, inland site). The two study years are treated separately. Values are only presented if at least 30 birds were caught each week.

Genomsnittliga fettvärden hos unga lövsångare i relation till breddgrad och typ av fångstlokal den första vecka som det genomsnittliga ruggstadiet var minst 3 respektive minst 5. (□ = ruggstadium 3, kust; ○ = ruggstadium 3, inland; ■ = ruggstadium 5, kust; ● = ruggstadium 5, inland). De två år som fettvärden samlades in behandlas var för sig. Värden presenteras bara när minst 30 fåglar fångats under varje vecka.

at Falsterbo, where on average 22.6% of adults (19/84) and 7.1% of juveniles (82/1159) had a fat score of 6. Overall proportions of more than 5% obese birds did not occur at any other site where large numbers of birds were trapped. Hence, Willow Warblers normally migrate through Sweden with relatively small fuel stores.

Retraps: In order to detect if any significant fat deposition took place at any of the sites, we asked for the proportion of retrapped Willow Warblers which had increased with 3 or more fat scores (Table 7). The proportion was low, between 2% and 5% for



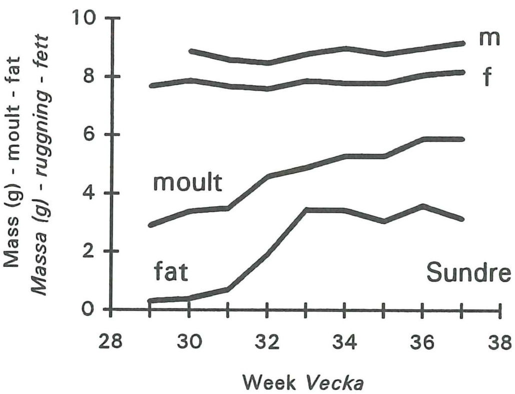


Fig. 5. Weekly averages of body mass (g, males and females treated separately), moult and fat score of juvenile Willow Warblers at a) Ånnsjön (site 3) and b) Sundre (site 14) in 1990. Values are only presented if at least 30 birds were caught each week.

Veckomedelvärden för kroppsmassa (g, separat för hanar och honor), ruggstadium och fett hos unga lövsångare 1990 vid a) Ånnsjön och b) Sundre. Värden presenteras bara när minst 30 fåglar fångats under varje vecka.

both adults and juveniles. However, on a few occasions a higher proportion of retraps with strong fat increase was reported, but total sample sizes were low.

Body mass

The average seasonal body mass of each age and sex class varied between sites and years (adult males 8.8–9.4 g, adult females 7.9–8.6 g, juvenile males 8.7–9.6 g, and juvenile females 7.7–8.7 g, Table 8). Males were heavier than females. Among adults where data sets met the selection criteria for both sexes in one year, the difference between males and females was 0.5–1.1 g (6 site/year cases), and among juveniles it was 0.6–1.2 g (43 site/year cases).

Age differences: The average values (sexes combined) were around 8.3–9.0 g in adults and 8.2–9.3 g in juveniles. At sites where both age groups were caught in sufficient numbers in a given year, adults were consistently, but only marginally, heavier than juveniles within each sex. In 18 out of 19 cases, adults were 0.1–0.4 g heavier on average (in one case average body mass was the same). The data set of adults was too small to make meaningful between-site and between-year comparisons.

Latitude and locality type: Among juveniles, average seasonal body mass tended to decrease towards southern Sweden, although there was a significant effect of latitude only for males in 1989. There were no significant effects of locality type on seasonal average body mass, and no trends in differences between absolute values either (T28).

We analysed body masses of juveniles at different ages (first week with average moult score > 3 and > 5; Table 9). Due to lack of data the effect of both latitude and locality type on average body mass could not be examined. Generally juvenile males and females weighed slightly more in northern Sweden. At the four most northern sites (sites 1–4) males and females weighed on average ≥9.0 g or ≥8.0 g, respectively (similar for both moult score groups). At the more southerly sites average body mass was generally ≤9.0 g and ≤8.0 g, for the two sexes respectively. In each of the five instances where five or more averages were available in a year for a given moult score (locality types combined), there was a clear trend towards lower average body masses at more southern latitudes, and significantly so in three cases (T29).

At sites where in one year sufficient birds of each sex were trapped in the two different moult stages, the difference in average mass was small (Table 9). Out of eight such cases, the difference was 0.1 g in six cases, 0.3 g in one case, and were equal in one case, with no trend that average body mass was higher in either of the moult score groups. However, only three sites (2, 3 and 14) contributed to this data set. The lack of differences in body mass between moult stages is in contrast to fat scores, which were significantly higher in moult stage 5 than in moult stage 3 (see above).

In conclusion, males were clearly heavier than females (although somewhat exaggerated due to how data were selected, see Methods), and within each sex, adults were normally heavier, although

Table 6. The number (N_6) and proportion (%) of Willow Warblers with fat score 6 at the different sites. Totals (N_{tot}) refer to birds trapped in the latter part of the season, starting with the first week juveniles had an average moult score of at least 5. The same time period was used for adults. The location of each site is shown in Fig. 1.

Antalet (N_6) och proportionen (%) lövsångare i fettklass 6 vid olika lokaler. Totalantalet (N_{tot}) anger antalet fåglar fångade i senare delen av säsongen, med början den vecka när medelruggstadiet hos ungfåglarna var minst 5. Samma tidsperiod är använd för adulta fåglar. De olika platsernas geografiska läge presenteras i Fig. 1.

		1989						1990					
		Ad			Juv			Ad			Juv		
	Locality *Plats*	N_6	N_{tot}	%	N_6	N_{tot}	%	N_6	N_{tot}	%	N_6	N_{tot}	%
2	Haparanda S	0	14	0.0	3	232	1.3	–	–	–	–	–	–
3	Ånnsjön	–	–	–	–	–	–	0	9	0.0	0	21	0.0
4	Eggegrund	–	–	–	–	–	–	0	87	0.0	3	986	0.3
6	Ässön	0	2	0.0	2	78	2.6	–	–	–	–	–	–
7	Kvismaren	0	1	0.0	2	92	2.2	0	6	0.0	0	29	0.0
9	Landsort	0	19	0.0	6	621	1.0	0	18	0.0	39	580	6.7
10	Hornborgasjön	–	–	–	–	–	–	1	3	33.3	0	64	0.0
11	Landsjön	0	5	0.0	0	11	0.0	0	1	0.0	1	16	6.3
13	Oskarshamn	0	4	0.0	4	12	33.3	–	–	–	–	–	–
14	Sundre	0	51	0.0	1	517	0.2	0	64	0.0	28	642	4.4
16	Ottenby	0	24	0.0	9	658	1.4	2	50	4.0	13	1077	1.2
17	Jordberga	–	0	–	0	27	0.0	–	–	–	0	92	0.0
18	Falsterbo	16	68	23.5	68	869	7.8	3	16	18.8	14	290	4.8
	Total *Summa*	16	188	8.5	95	3117	3.0	6	254	2.4	98	3797	2.6

Table 7. Number of adult and juvenile Willow Warblers which increased at least 3 fat scores (N_{+3}) between ringing and retrapping (the same season) at each site. The number of retraps (N_k), and the percentage of retraps that increased at least 3 fat scores, are also shown. The location of each site is shown in Fig. 1.

Antalet gamla och unga lövsångare som ökade 3 eller fler fettsteg (N_{+3}) mellan märkning och återfångst (samma säsong) vid de olika lokalerna. Antalet återfångade fåglar (N_k), samt andelen (%) kontroller som ökade med 3 eller fler fettsteg, presenteras också. De olika platsernas geografiska läge presenteras i Fig. 1.

		1989						1990					
		Ad			Juv			Ad			Juv		
	Locality *Plats*	N_{+3}	N_k	%	N_{+3}	N_k	%	N_{+3}	N_k	%	N_{+3}	N_k	%
1	Ammarnäs	0	8	0	0	39	0	0	11	0	0	122	0
2	Haparanda S	2	11	18	2	125	2	1	48	2	3	88	3
3	Ånnsjön	1	100	1	3	75	4	7	88	8	2	142	1
6	Ässön	0	0	0	1	5	20	0	0	0	0	11	0
7	Kvismaren	0	0	0	3	9	33	0	1	0	0	12	0
9	Landsort	0	0	0	1	33	3	0	2	0	1	20	5
10	Hornborgasjön	0	1	0	1	13	8	0	2	0	0	11	0
11	Landsjön	–	–	–	–	–	–	0	3	0	0	3	0
13	Oskarshamn	0	0	0	0	0	0	0	0	0	3	10	30
14	Sundre	0	0	0	0	42	0	0	2	0	2	71	3
15	Kalmar	0	0	0	0	1	0	–	–	–	–	–	–
16	Ottenby	0	1	0	0	5	0	0	0	0	0	17	0
17	Jordberga	0	0	0	0	4	0	–	–	–	0	2	0
18	Falsterbo	0	0	0	2	43	5	0	0	0	0	20	0
	Total *Summa*	3	123	2	13	394	3	8	157	5	11	529	2

Table 8. Average body mass (g) of adult and juvenile Willow Warblers during the autumns of 1988–1990. Males and females are treated separately. Data are only shown when more than 30 birds of an age/sex group were caught within one season. The location of each site is shown in Fig. 1.

Genomsnittlig kroppsmassa (g) hos gamla och unga lövsångare höstarna 1988–1990. Hanar och honor presenteras var för sig. Medelvärden visas endast om minst 30 fåglar i en köns- och åldersgrupp fångats under säsongen. De olika platsernas geografiska läge presenteras i Fig. 1.

		Males *Hanar*						Females *Honor*					
		1988		1989		1990		1988		1989		1990	
	Locality *Plats*	Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv
1	Ammarnäs	–	9.2	–	9.4	–	9.4	–	8.3	–	8.4	–	8.4
2	Haparanda S	–	9.2	–	9.2	–	9.2	–	8.2	–	8.2	8.6	8.3
3	Ånnsjön	–	8.7	9.4	9.0	9.1	9.1	8.3	7.9	8.5	8.2	8.6	8.2
4	Eggegrund	–	9.0	–	–	9.2	9.2	7.9	7.8	–	–	8.1	8.1
5	Idö, Mälaren	–	–	–	9.0	–	9.0	–	–	–	8.1	–	8.0
6	Ässön	–	9.0	–	8.9	–	8.8	–	8.0	–	7.9	–	7.9
7	Kvismaren	–	8.8	–	8.8	–	8.7	–	7.9	–	7.9	–	7.8
8	Stegsholm	8.8	8.8	–	–	–	–	–	7.9	–	–	–	–
9	Landsort	–	8.8	–	9.1	–	9.2	–	7.9	–	8.0	–	8.0
10	Hornborgasjön	–	8.8	–	8.9	–	8.8	–	7.9	–	7.9	–	7.9
11	Landsjön	–	9.2	–	9.1	–	9.2	–	8.2	–	8.4	–	8.3
12	Nidingen	8.8	8.7	–	–	–	–	7.8	7.7	–	–	–	–
13	Oskarshamn	–	9.8	–	–	–	9.1	–	9.1	–	8.5	–	8.2
14	Sundre	8.7	8.7	9.1	8.8	–	8.9	7.8	7.7	–	7.8	8.2	7.9
16	Ottenby	–	8.7	–	9.0	–	9.6	–	7.7	–	7.9	–	8.7
17	Jordberga	–	–	–	8.8	–	8.5	–	–	–	7.8	–	7.9
18	Falsterbo	9.0	8.9	9.4	9.0	–	8.9	8.1	7.9	–	7.9	–	8.0

only marginally so, than juveniles. For juveniles, average body masses were lower at southern localities, and the trend was the same when treating birds in different moult stages separately. Older juveniles (moult stage 5) were not heavier than younger juveniles (moult stage 3). The average body mass in juveniles did not seem to differ between inland and coastal sites.

Seasonal trends within sites: Among juvenile males, four out of eight within-site seasonal trends in body mass were negative and four were positive. Five sites were used for this analysis (sites 2, 3, 14, 16 and 18). For juvenile females, eight out of eleven trends were positive. Only three within-site trends were significant, all of them positive and all at Ottenby (site 16): males in 1990, and females in 1989 and 1990 (T30). Apart from Ottenby, there were only weak indications, if any, that body mass increased during the autumn within a site. The six sites (sites 2, 3, 10, 14, 16 and 18) include both northern and southern sites, of both coastal and inland location. The lack of seasonal body mass trends is in contrast to the clear trends in fat score (Fig. 5). Sample sizes of adults were not large enough to allow a similar analysis.

Retraps: The numbers and proportions of retrapped Willow Warblers which increased by more than 1.0 g between ringing and retrapping was only between 2% and 5% for both adults and juveniles (Table 10). However, at a few sites each year, 10–50% of retraps increased in mass by more than 1.0 g, although sample sizes were small.

Discussion

Before drawing general conclusions about the autumn migration of Swedish Willow Warblers, it is important to discuss how representative the set of participating ringing sites are for such a study. There were equal numbers of coastal and inland sites, and both the latitudinal extent (1200 km) and the relatively even distribution of sites in southern Sweden are satisfactory. However, there are relatively few ringing sites in northern Sweden. Of the four sites (1–4) dealing mainly with *acredula* birds, two are coastal and two inland. Also, at each of these sites ringing activity was high (although one year is missing at site 4). It is probable that these sites

Table 9. Average body mass of juvenile male and female Willow Warblers during the first week at each site when birds reached an average moult score (MS) of at least 3.0 and 5.0. Data are only shown when more than 30 birds were caught in one week. The median day of the week from which the data are collected is also given. The location of each site is shown in Fig. 1.

Genomsnittlig kroppsmassa hos unga hanar och honor av lövsångare i olika stadier av kroppsruggning (MS). Värdena som presenteras är de genomsnittliga kroppsmassorna den första vecka som fåglarna i genomsnitt var i ruggningstadium 3.0 respektive 5.0. Medelvärden visas endast om minst 30 fåglar fångats på en vecka. Datumen motsvarar torsdagen i den vecka från vilken värdena är hämtade. De olika platsernas geografiska läge presenteras i Fig. 1.

	Males *Hanar*						Females *Honor*					
	1988		1989		1990		1988		1989		1990	
Locality *Plats*	MS>3	MS>5	MS>3	MS>5	MS>3	MS>5	MS>3	MS>5	MS>3	MS>5	MS>3	MS>5
1 Ammarnäs	9.1 11 Aug	–	–	–	9.5 9 Aug	–	8.1 11 Aug	–	–	–	8.4 9 Aug	–
2 Haparanda S	9.1 11 Aug	9.1 25 Aug	9.3 10 Aug	–	9.3 9 Aug	–	8.2 11 Aug	8.1 25 Aug	8.4 10 Aug	–	8.2 9 Aug	–
3 Ånnsjön	8.7 4 Aug	8.4 18 Aug	–	–	9.0 9 Aug	–	7.9 4 Aug	7.8 18 Aug	8.1 17 Aug	–	8.0 9 Aug	–
4 Eggegrund	–	–	–	–	–	8.9 16 Aug	–	–	–	–	–	8.0 16 Aug
6 Ässön	–	–	–	–	8.9 26 Jul	–	–	–	7.9 20 Jul	–	7.9 26 Jul	–
8 Stegsholm	–	–	–	–	–	–	–	8.2 11 Aug	–	–	–	–
9 Landsort	–	–	–	–	–	–	–	7.7 18 Aug	–	–	–	–
10 Hornborgasjön	8.8 21 Jul	–	8.9 20 Jul	–	–	–	7.8 21 Jul	–	7.9 20 Jul	–	7.9 19 Jul	–
14 Sundre	–	8.8 25 Aug	–	8.8 24 Aug	8.9 26 Jul	9.0 23 Aug	7.7 28 Jul	7.8 25 Aug	7.8 27 Jul	7.9 24 Aug	7.9 26 Jul	7.8 23 Aug
16 Ottenby	–	–	–	–	–	8.7 23 Aug	–	7.4 11 Aug	–	7.8 17 Aug	–	7.9 23 Aug
18 Falsterbo	–	–	–	8.9 10 Aug	–	8.9 9 Aug	–	–	–	8.0 10 Aug	–	8.0 9 Aug

therefore gave representative and reliable results, which is reassuring for the latitudinal analyses that form an important part of this study.

Age proportions

The high average proportion of juveniles reported at both coastal and inland sites (93%), may not reflect the true age proportions of the populations. For example, even if Willow Warblers produce five or six fledglings per pair (Cramp 1992) and all these survive until autumn migration (which seems very unlikely), the proportion of juveniles in the population would only be around 70% or 75%.

It is well-known that ringing sites located at geographically exposed places such as islands and tips of peninsulas generally attract a disproportionally large number of juveniles (reviewed by Pettersson 1983). Equally high proportions of juvenile Willow Warblers have been reported before (Hedenström & Pettersson 1984). This may well be the result of the relative inexperience of juvenile birds, unfamiliar with geographical barriers and unaware of the fuel stores required to negotiate them. Therefore unplanned groundings could take place at poor coastal stopover sites more often than with experienced adults (e.g. Lindström & Alerstam 1986). The high proportions of juveniles at many of the coastal sites could therefore be expected. A considerably lower proportion of juveniles (79%) were trapped in 1988 at Nidingen (site 12), a small island off the western coast of Sweden. Correct ageing of these birds was confirmed by a high prevalence of interrupted secondary moult (Hedenström et al. 1995). Similar unusual age proportions have been recorded in other years at this site (Uno Unger, personal communication). Large numbers of Willow Warblers at Nidingen often occur when sudden and unpredictable weather changes take place. This may ground a more representative sample of migrants aloft which normally would pass unnoticed (Uno Unger, personal communication). Data from ringing activities at extreme geographical localities, which could be either representative or highly unrepresentative of the population studied, need to be treated with caution.

Inland localities may represent more "normal" stopover sites for Willow Warblers, therefore the proportion of juveniles ought to be lower at inland sites. However, the proportion of juveniles was very high also at these sites. Willow Warblers breed in the catching areas at most inland sites with ringing carried out prior to the migration period. At this time, juveniles undergo post-juvenile moult and engage in non-directed movements which make them easy to catch in large numbers. Adults, in contrast, undertake a full-moult and are difficult to catch, mainly due to their reluctance or inability to fly (Haukioja 1971). They are probably also more stationary than juveniles. The combined effect will be a too high proportion of juveniles in the catch. The trend that the proportion of juveniles within each site decreased as the season progressed supports this conclusion. However, at the inland sites during the last part of the migratory season, when adult moult should be complete, the proportion of juveniles was still well above 90%.

It is not possible with the present data to explain the high proportions of juveniles at both coastal and inland sites. The possibility that inland sites included in this study were not representative of "normal" Willow Warbler stopover sites exists. They may well be situated at "ecological islands". Alternatively, adults and juveniles may employ different migration strategies. The tendency was for adults to carry slightly more fat than juveniles, which would enable them to undertake longer flight distances, possibly resulting in fewer stopovers within Sweden. This would result in fewer adults being caught at bird observatories than the actual numbers present in the population. Also, adults have a more pointed wing than juveniles, which allows them to fly longer on a given fuel store (Norman 1997).

Timing of migration in relation to age, sex and subspecies

The chosen sampling period (mid July to late September) includes the latter part of the moult cycle (for both adults and juveniles), as well as the active migration period. Willow Warbler movements in autumn start as short non-directed flights during the late stages of moult (at least for juveniles) and progressively turn into longer directed migratory flights (Norman & Norman 1985). It is difficult to define when a bird has started its directed migration. Describing the timing of migration is therefore difficult, especially at many of the inland sites where local moulting birds and migrating birds are included in the catch. Indeed, Willow Warblers were trapped on average 2–4 weeks earlier at inland than at coastal sites, even though trapping seasons were similar.

Age: At coastal localities which deal mainly with birds on migration, adults were trapped on average 0–7 days later (sometimes more) than juveniles. The complete post-breeding moult of adults, which includes moult of flight feathers (Underhill et al. 1992), sets a time limit on how early migration can commence. Juveniles, do not moult flight feathers during post-juvenile moult, and may be able to commence migration earlier than adults. Later in the autumn adults seem to have caught up and even bypassed the juveniles through continental Europe (Hedenström & Pettersson 1987). In long-distance migrant passerine species where adults do not undertake a full post-nuptial moult, adults depart on their autumn migration much earlier than the juveniles (e.g. Koskimies & Saurola 1985, Fransson 1995, Nielsen & Rhönnstad 1996).

Sex: Among adults there were no significant or consistent differences between average trapping date of males and females. The same pattern was found by Niemeyer (1969) analysing autumn passage over Helgoland in northern Germany. Although females undergo their post-breeding moult on average 5–10 days later than the males (Norman 1990, Underhill et al. 1992, Bensch & Grahn 1993), they are obviously able to adjust their moult in such a way that they can depart at the same time as males. An important reason may be that they are more prone to depart with some unmoulted secondaries (Hedenström et al. 1995).

Table 10. Number of adult and juvenile Willow Warblers which increased at least 1.1 g in body mass (N_+) between ringing and retrapping (the same season) at each site. The number of retraps (N_k), and the percentage of retraps that increased at least 1.1 g in body mass, are also shown. The location of each site is shown in Fig. 1.

Antalet gamla och unga lövsångare som ökade i vikt mer än 1.0 g (N_+) mellan märkning och återfångst (samma säsong) vid de olika lokalerna. Antalet återfångade fåglar (N_k), samt andelen (%) kontroller som ökade med mer än 1.0 g, presenteras också. De olika platsernas geografiska läge presenteras i Fig. 1.

		1988						1989			
		Ad			Juv			Ad			
	Locality *Plats*	N_+	N_k	%	N_+	N_k	%	N_+	N_k	%	N_+
1	Ammarnäs	0	12	0	1	83	1	0	8	0	0
2	Haparanda S	1	8	12	7	59	12	1	11	9	7
3	Ånnsjön	0	26	0	2	79	2	1	97	1	1
5	Idö, Mälaren	–	–	–	–	–	–	0	0	0	0
6	Ässön	0	0	0	0	9	0	0	0	0	1
7	Kvismaren	0	3	0	0	12	0	0	0	0	2
9	Landsort	0	0	0	1	4	25	0	0	0	0
10	Hornborgasjön	0	1	0	1	30	3	0	1	0	0
11	Landsjön	0	0	0	0	20	0	–	–	–	–
12	Nidingen	0	3	0	13	85	15	–	–	–	–
13	Oskarshamn	0	0	0	–	–	–	0	0	0	0
14	Sundre	0	0	0	0	75	0	0	2	0	0
15	Kalmar	–	–	–	–	–	–	0	0	0	0
16	Ottenby	0	0	0	0	18	0	0	1	0	1
17	Jordberga	–	–	–	–	–	–	0	0	0	0
18	Falsterbo	0	1	0	0	28	0	0	0	0	3
	Total *Summa*	1	54	2	25	502	5	2	120	2	15

Subspecies: Based on trapping data from Falsterbo (site 18) and Ottenby (site 16), Högstedt & Persson (1982) suggested that juveniles of the two subspecies commenced migration at a similar age. The moult scoring system used in this paper is a potentially strong tool when estimating age (in days) of birds at different sites and could shed further light on this question.

At Ammarnäs (site 1), median date of trapping occurs in the first week of August. In this period of peak movement, average moult scores were between 2.6 and 3.1. By the 15 August most juvenile Willow Warblers have departed and average moult score is between 3 and 4. This suggests to us that northern Willow Warblers are mobile when about 27–32 days old, and leave the breeding area at an age of 32–37 days. At Falsterbo (site 18), few birds were trapped in moult stages 1–3 (0.4% in 1988, 2% in 1989, and 3% in 1990). Willow Warblers breed in good numbers within a few km, and at 20 km or more to the NE the breeding population is dense. If these patterns are representative for northern and southern Willow Warblers, the first exploratory or migratory movements among juveniles occur earlier in the northern subspecies. Juvenile British Willow Warblers, of the *trochilus* subspecies, do not start to disperse until in late post-juvenile moult (Lawn 1984, Norman 1994), which confirms the pattern found at Falsterbo.

There was no significant correlation between latitude and median trapping date at the coastal sites. At Haparanda Sandskär (site 2), a small island situated 20 km from the mainland, juvenile Willow Warblers were trapped relatively early. The median date of trapping in 1988–1990 varied around 18 August, similar to Falsterbo (site 18), 1200 km to the south. Since breeding is around 14 days later in northern compared to southern Sweden (Högstedt & Persson 1982), it follows that juveniles of northern stock on migration should be about 14 days younger than those in southern Sweden. During week 33 (peak migration time), average moult score was 4.3, 3.6 and 3.3 (age 35–40 days) at Haparanda Sandskär and 5.6, 5.5 and 5.4 (age 50–55 days) at Falsterbo. Obviously, only northern birds are trapped at Haparanda Sandskär, whereas mainly southern birds appear at Falsterbo. The average moult score at peak passage suggest that when migration starts, juvenile Willow Warblers of the northern subspecies are about two weeks younger than their southern conspecifics.

In conclusion, these results indicate that juvenile Willow Warblers of the northern subspecies *acredula* commence migration at an earlier age than birds of the southern subspecies *trochilus*, which is in contrast to the conclusion by Högstedt & Persson (1982). Experiments with caged Willow Warblers show that *acredula* juveniles undergo migratory restlessness at an earlier age than southern birds (Gwinner et al. 1972). It is possible Högstedt & Persson (1982) drew this probably erroneous conclusion because as a measure of the onset of migration for northern birds they used a median value trapping date from Hartsö-Enskär, a bird observatory near site 9 in southern Sweden (Fig. 1). When the northern birds pass through this area many may already have travelled 500–1000 km, which on average is much further than southern birds at Falsterbo. Given that the early part of migration is slow (about 40 km d^{-1}, Hedenström & Pettersson 1987), the median date at Hartsö-Enskär may not be representative for the onset of migration in northern birds. A similar pattern to Sweden seems to be present in the British Isles population with northern birds starting migration at an earlier age than southern birds (Lawn 1984, Norman 1994).

		1990					
Juv		Ad			Juv		
N_k	%	N_+	N_k	%	N_+	N_k	%
39	0	0	11	0	0	122	0
125	6	4	48	8	5	89	6
83	1	4	86	5	0	147	0
1	0	0	5	0	0	2	0
5	20	0	0	0	0	11	0
8	25	0	1	0	0	12	0
29	0	0	2	0	2	19	11
13	0	0	2	0	3	11	27
–	–	0	3	0	0	3	0
–	–	–	–	–	–	–	–
0	0	0	0	0	5	10	50
42	0	0	2	0	0	71	0
1	0	–	–	–	–	–	–
5	20	0	0	0	0	17	0
4	0	–	–	–	0	2	0
43	7	0	0	0	0	20	0
398	4	8	160	5	15	536	3

Our interpretation is dependent on the moult scoring system being representative for both subspecies. Jenni & Winkler (1994) argued that this may not be the case, since northern birds may start moult earlier, moult faster and in a different sequence to southern birds. However, if southern birds are older than the moult score predicts (due to a later start and slower progress of moult), then the difference in timing of migration between subspecies would be even greater, since the moult scoring was calibrated on the *acredula* subspecies at site 1 (Bensch & Lindström 1992).

Wing lengths

As no comparisons were made between ringers from the different sites, inter-observer variability may influence the values reported. Therefore, the absolute values at any given site should be treated with some caution. However, we believe that the large number of sites will enable geographical trends to be detected, and that seasonal trends within sites should be fairly reliable.

Two previously recognised patterns of wing length variation among Swedish Willow Warblers were confirmed: adults had on average longer wings than juveniles (Norman 1983) and northern birds had longer wings than southern birds (Salomonsen 1945, Fonstad & Hogstad 1981). The latter was only confirmed for juveniles, though. In adults, the lack of difference may at least partly be explained by the fact that many northern adults were trapped when their primaries were worn (and hence shorter). Possibly, a too small data set, especially when related to inter-observer variability and the higher risk of varying proportions of the two sexes in different samples, added further uncertainty to the analysis.

Average wing lengths of juveniles increased within each site as the season progressed, although only significantly in a few cases. This trend has also been found in earlier studies at various localities (Petersson 1984, Hedenström & Pettersson 1984, Pettersson & Hedenström 1986, Betzholtz 1988), and probably reflects the seasonally later passage of longer-winged northern birds. This pattern was particularly obvious at Sundre (site 14) and Ottenby (site 16), the two most south-eastern sites in Sweden, where both subspecies are known to occur in high numbers (Hedenström & Pettersson 1984, Nissling et al. 1990). Whether the seasonal increase in wing length at some sites could be explained by a sequential passage of longer-winged birds *within* a subspecies (for example males) passing later, is not known.

Post-juvenile moult

Since age, which is based on the moult scoring of juvenile Willow Warblers (Bensch & Lindström 1992), is easier to relate to than the moult scores themselves, we will mainly refer to age rather than moult score in this section.

On average for the whole season, juveniles were younger at inland than at coastal sites. This reflects the trapping of many moulting birds in early autumn, in addition to migrants trapped later on. In the early part of the season (around 10 August), the age of birds at coastal and inland sites was similar. This was probably due to the fact that the migratory season had not really commenced by then. Two weeks later during peak migration time (around 24 August), the picture was less clear. In 1990, birds at coastal sites were on average older than birds at inland sites. This is to be expected, given that mainly older birds depart on migration and occur at coastal sites. However, this pattern was not present in 1988.

Seasonal averages showed that juvenile birds were older the further south in Sweden they were trapped. This relationship was present even when looking at only the early part of the season (around 10 August), probably reflecting the earlier start of the breeding season at the more southerly latitudes (cf. Högstedt & Persson 1982). Later in the season (around 24 August) there was a relationship between latitude and average age, but only in 1990 (not in 1988 and 1989). The reason why the effect of latitude was not present in two out of three years was probably due to methodology: birds having reached the maximum moult score of 6 cannot increase this any further, but they undoubtedly get older. Thus, averages already close to 6 in southern Sweden cannot increase further later in autumn, while lower averages in northern Sweden can still increase. This explanation is probably relevant at least for 1988, which probably was the earliest breeding season of the three years.

Energy stores for migration – fat score and body mass

Fat is the main source of energy for migration, although some storage of protein also takes place (Lindström & Piersma 1993). One aim of the present project was to describe and analyse the size of energy stores of Willow Warblers throughout early autumn. There are two easy ways of obtaining such information: to weigh the birds and to score visual fat loads. Several studies have reported a good correlation between fat score and true fat load (Rogers 1991, Kaiser 1993, Lundgren et al. 1995), and between fat score and body mass (Koskimies & Saurola 1985, Pettersson & Hasselquist 1985, Ellegren 1989). These studies were conducted on homogenous samples of birds in migratory disposition and body mass alone gave good indications of the general size of energy stores. This is advantageous since scoring fat is more difficult than weighing a bird, especially for inexperienced ringers, and will inevitably be somewhat subjective. But there are at least two good reasons to score visual fat loads.

First, prior to the onset of migration, both adults and juveniles undergo moult. During this moult birds have an increased amount of water (blood) in their bodies (Newton 1968, Chilgren 1977). Thus, significant changes in body mass during moult may have little to do with changes in fat stores (Lindström et al. 1994). This is shown at the Ånnsjön and Sundre sites: where birds at the end of post-juvenile moult showed increasing fat stores, but body mass remained more or less constant. It is likely that visual fat score gives a good measure of the size of fat stores, regardless of the moult condition, but this needs investigating. For moulting birds, visual fat score is a much better predictor of fat stores than body mass. If body mass alone had been used in this study, then the outcome would probably have been that no deposition of energy stores for migration occurs in Swedish Willow Warblers.

Second, visual fat scores may be less sensitive than body mass to variation in body size. For example, a large or a small bird, with fat scores of 5, probably have proportionally sized fat stores, whereas the body mass of the larger bird would be higher. If body size was not completely corrected for (cf. Ellegren 1989), the size of fat stores based on body mass could be overestimated for larger birds. *Ph.t.acredula* are larger than *Ph.t.trochilus*, with males larger than females. Because different proportions of populations and sexes may bias estimates of fat stores predicted from body mass, fat scores are probably affected to a much smaller degree. The following discussion on energy stores of autumn Willow Warblers in Sweden mainly refers to fat score data.

Age differences: Too few adults were trapped to allow large scale comparisons with juveniles. There were indications that the two age groups had similar fat stores in northern Sweden, whereas adults had larger stores than juveniles in southern Sweden. It could be that during moult and in the early phase of autumn migration fat stores are similar, but in later phases of migration, adults carry larger fat stores.

Previous studies of passerine migrants at stopover sites have shown that adults often carry more fat than juveniles (for example, Veiga 1986, Ellegren 1991, Nielsen & Rhönnstad 1996).

The effect of latitude, locality type and juvenile age: Seasonal averages showed that both adults and juveniles were fatter the further south in Sweden they were trapped, and also that the birds were generally fatter at coastal than at inland sites. However, since northern and inland birds (juveniles) were on average younger when trapped, it is necessary to look at equally-aged birds when interpreting the pattern of fat deposition in relation to migration of individual birds. Relatively few adults were trapped, and from the way data were reported we were unable to separate fat scores of moulting and non-moulting birds. Therefore, the following discussion is concerned with juveniles only.

Juveniles in mid post-juvenile moult (moult stage 3, average age 32 days) had on average very small fat stores throughout Sweden. Similar small fat loads during mid post-juvenile moult has been reported for Willow Warblers (Baggott 1975), Bluethroats *Luscinia svecica* (Lindström et al. 1985), Sedge Warblers *Acrocephalus schoenobaenus* and Reed Warblers *A. scirpaceus* (Koskimies & Saurola 1985, Nielsen & Rhönnstad 1996) and is probably a general pattern among juvenile passerines. Several reasons may account for these small fat stores. Ringing recoveries of British Willow Warblers show that in the first part of the autumn juveniles are moving in all possible directions (Norman & Norman 1985). If this period serves as a kind of exploration period with no long flights taking place (Baker 1993, Nielsen & Bensch 1995), large fat stores would not be required. However, it is also possible that in juveniles in early moult a tight energy budget sets a limit to the amount of fat that can be stored. Moulting a largely new body plumage may be highly costly (Lindström et al. 1993). In addition, due partly to foraging inefficiency, food may not be readily available to juveniles. Weathers & Sullivan (1989) studied the time and energy budget of newly independent juvenile Yellow-eyed Juncos *Junco phaenotus*, and found that they foraged for more than 90% of the day in order to meet their energy requirements for survival. This leaves a narrow energy margin for fat deposition.

At the last stage of moult (moult stage 5, average age 44 days), juvenile Willow Warblers were on average significantly fatter than at earlier stages. This certainly reflects the onset of migration. No effect of latitude on average fat scores was evident at this stage. Consequently, Willow Warblers appear to lay down fat when ready for migration, but the size of these fat stores do not increase during the migratory journey within Sweden. Alternatively, if northern and southern trapping sites catch mainly local birds, then birds of the two subspecies, carry similar fat loads while on migration through Sweden.

Fat scores were higher at coastal than at inland sites, even though many of the coastal birds had probably undertaken one nights migration flight before being trapped. Birds caught inland may have included a higher proportion of birds present for more than one day. This suggests that when birds are ready to leave Sweden, they may top up with additional fat. Due to the south-westerly and south-south-easterly migration directions of the two subspecies (Hedenström & Pettersson 1987), all or most of the coastal sites may trap birds in migration condition for longer non-stop flight over open sea. Such "top-up" fattening occurs in Sweden, but was not often recorded: only a few percent of retraps showed significant increases in fat score and only a few percent of the birds had fat score 6. Data from more years and more sites may be necessary to reveal where in Sweden, and to what extent, such fattening occurs.

The higher fat loads in Willow Warblers at coastal sites are in contrast to Robins *Erithacus rubecula* and Goldcrests *Regulus regulus* at Ottenby (site 16), where birds trapped at coastal localities had less fat than birds trapped inland (Pettersson & Hasselquist 1985). The higher fat loads in inland birds in these species could be due to representative fattening being recorded at inland places (Pettersson & Hasselquist 1985), and/or that a high proportion of coastal catches included "emergency landings" of birds with disproportionally small fat stores (cf. Lindström & Alerstam 1986, Åkesson et al. 1996). Ehnbom et al. (1993), however, found that coastal Robins (at Falsterbo, site 18) in general were fatter than those caught 200 km inland.

Even though birds were clearly fatter during the latter part of moult, the average fat scores throughout Sweden at moult stage 5 were relatively small (1.5–3.7), and very few fat birds were trapped. This suggests Willow Warblers adopt a "hopping" migration strategy through Sweden (sensu Piersma 1987), storing fat for only short flights at a time, at least until they approach the crossing over the Baltic Sea. Such a pattern has been suggested before for both Swedish (Hedenström & Pettersson 1987) and British Willow Warblers (Norman 1987).

Lundgren et al. (1995) found that juvenile Willow

Warblers with fat score 3 and 4 carry around 0.7 g fat (range 0.3–1.1 g). Assuming that the average bird in fat score 3–4 weighs 8.5 g, the fat load would be proportional to about 9% of lean body mass. The corresponding value for British juveniles on migration has been reported to be 15% (Baggott 1986). The latter value would be sufficient for somewhat more than one nights flight (Baggott 1986). The average Swedish Willow Warbler would then have fat for about one nights flight. However, if birds arriving at coastal sites had already undertaken one nights migration flight, then many must have set out on migration with fat loads sufficient for at least two nights of migration. A similar pattern was described for Robins and Goldcrests at Ottenby, Sweden (Pettersson & Hasselquist 1985).

Not all passerines in northern Europe adopt the strategy of small fat loads and short flights in autumn. Juvenile British Sedge Warblers *Acrocephalus schoenobaenus* and Reed Warblers *A. scirpaceus* (Bibby & Green 1981) put on huge amounts of fat already in southern England and northern France, and then seem to make one long flight to south of the Sahara (Sedge Warblers) or the Iberian peninsula (Reed Warblers). These birds clearly adopt a "jumping" strategy (Piersma 1987). Birds of the same two species at Lake Kvismaren, Sweden (site 7), carry smaller fat loads in autumn than British birds, and at Kvismaren Reed Warblers carry more fat than Sedge Warblers (Nielsen & Rhönnstad 1996). Also Finnish Sedge Warblers carry smaller fat loads than their British conspecifics (Koskimies & Saurola 1985). These examples clearly show that even during the early part of autumn migration of passerines in northern Europe, fat deposition strategies vary considerably between species and populations of the same species.

Body mass: Data on body mass add little information to the general knowledge about energy stores obtained from fat scores. Adults weighed on average somewhat more than juveniles, due in part to adults being larger, but also because adults carry more fat. Juveniles in northern Sweden weighed somewhat more than southern birds, most likely due to their larger size (fat scores were similar). In contrast to fat score, body mass within sites did not generally increase with season. The reason for this has been discussed above. As with fat score, only few retrapped birds increased significantly in mass.

The average body masses of 8.3–9.3 g in Sweden are close to average autumn values reported in other studies in northern Europe, for example: 8.7 g in Sweden (Betzholtz 1989), 8.1–9.4 g in Britain (Baggott 1975, 1986, Norman 1987), 8.3–8.4 g in France (Bibby & Green 1983), see also Cramp (1992). Prior to crossing the Sahara much higher averages values have been found: 9.2–10.5 g (Cramp 1992). However, Willow Warblers in captivity regularly reach average body masses of 14 g, with individuals reaching above 17 g (Gwinner 1969, Gwinner et al. 1971, 1972). Clearly, Willow Warblers migrating through Sweden in autumn have energy reserves far below their physiological capacity.

Concluding remarks

Hundreds of people were involved in "Project Willow Warbler". The participation of so many individuals is of course a prerequisite for a successful result in such a project, but also increases the variation in data quality. However, during the analysis and preparation of this paper we were amazed by the very low occurrence of obvious errors. The consistency in the data set as a whole was remarkable. This should lend credibility to the whole project, and reassure those hesitating to embark on similar enterprises. Large scale projects involving both amateurs and professionals can indeed be successful.

In addition to the "standard" set of measurements in field studies of migration ecology (wing length, fat scoring and body mass), the participants used a scale for describing the progress of post-juvenile moult, from which it is possible to age juvenile birds (Norman 1990, Bensch & Lindström 1992). We hope that the present study shows the latent power of such a scale when studying various aspects of passerine ecology. Topics such as average age at different localities, relative timing of subspecies migration, and fat loads and body masses of birds on active migration, could not have been dealt with in detail without the use of this scale.

For practical reasons it was not possible to present all the data analysed, for example the seasonal trends of various factors within sites. However, these data can be obtained from the authors upon request.

We have only analysed data based on averages. Many more detailed questions can be answered when analysing a data set containing information on individual birds. Also, many analyses could not be made due to the way data were reported. Thus, many interesting questions remain unanswered, and several can be dealt with by detailed analysis of data from a single site alone. Suggestions for further studies are listed in Appendix 3. We hope that the outcome of "Project Willow Warbler" will stimulate further co-operation between bird observatories and ringers, continued data collection of high standards, and, even more important, data analysis and presentation in appropriate journals.

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	Locality *Plats*	Co-ordinates Koordinater	
1	Ammarnäs	65.58 N	16.05 E
2	Haparanda S	65.34 N	23.46 E
3	Ånnsjön	63.16 N	12.28 E
4	Eggegrund	60.42 N	17.11 E
5	Idö, Mälaren	59.23 N	16.48 E
6	Ässön	59.16 N	15.25 E
7	Kvismaren	59.10 N	15.25 E
8	Stegsholm	59.06 N	18.16 E
9	Landsort	58.46 N	17.52 E
10	Hornborgasjön	58.19 N	13.34 E
11	Landsjön	57.52 N	14.21 E
12	Nidingen	57.18 N	11.54 E
13	Oskarshamn	57.16 N	16.24 E
14	Sundre	56.53 N	18.11 E
15	Kalmar	56.40 N	16.19 E
16	Ottenby	56.12 N	16.24 E
17	Jordberga	55.26 N	13.25 E
18	Falsterbo	55.23 N	12.49 E

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Appendix 1

Autumn catching periods at the study sites in 1988–1990 for years when data were reported. CI refers to the average weekly catching intensity: H = 5–7 days/week, M = 3–4 days/week, and L = 1–2 days/week.

Perioder under höstarna 1988–1990 då fångst bedrivits vid de olika fångststationerna de år som data redovisats inom projektet. Under CI redovisas den genomsnittliga fångstintensiteten: H = 5–7 dagar/vecka, M = 3–4 dagar/vecka, och L = 1–2 dagar/vecka.

1988		1989		1990	
Catching period *Fångstperiod*	CI	Catching period *Fångstperiod*	CI	Catching period *Fångstperiod*	CI
18 Jul–31 Aug	H	17 Jul–18 Aug	H	18 Jul–13 Aug	H
31 Jul–20 Oct	H	05 Aug–23 Sep	H	27 Jul–30 Sept	H
16 Jul–28 Aug	H	02 Jul–10 Sep	H	30 Jun–02 Sep	H
10 Aug–30 Oct	H	–		01 Aug–30 Sep	L
21 Jul–11 Sep	L	30 Jun–24Sep	L	21 Jul–30 Sep	L
14 Jul–26 Sep	L	17 Jul–27 Sep	L	22 Jul–29 Sep	L
27 Jun–28 Sep	M	23 Jun–28 Sep	M	16 Jul–29 Sep	M
23 Jul–30 Oct	L	–		–	
02 Aug–02 Oct	M	13 Aug–01 Oct	H	23 Jul–30 Sep	H
21 Jul–30 Sep	H	17 Jul–30 Sep	H	16 Jul–29 Sep	H
20 Jul–24 Sep	M	18 Jul–30 Sep	M	16 Jul–29 Sep	M
01 Jul–04 Nov	H	–		–	
23 Jul–17 Sep	L	15 Jul–18 Sep	M	07 Jul–29 Sep	M
25 Jul–30 Oct	H	24 Jul–17 Sep	H	22 Jul–16 Sep	H
–		07 Aug–20 Sep	L	–	
01 Jul–15 Nov	H	01 Jul–15 Nov	H	01 Jul–15 Nov	H
–		16 Jul–01 Oct	M	15 Jul–02 Oct	L
21 Jul–10 Nov	H	21 Jul–10 Nov	H	21 Jul–10 Nov	H

Appendix 2

Statistical test referred to in the text. *Statistiska beräkningar hänvisade till i texten.*

T 1. ANOVA, $F_{[2,36]} = 0.4$, $p = 0.64$.
T 2. ANCOVA, latitude: $F_{[1,15]} = 2.0$, $p = 0.17$; locality type $F_{[1,15]} = 0.1$, $p = 0.74$.
T 3. ANCOVA, 1988: latitude $F_{[1,5]} = 2.5$, $p = 0.18$, locality type $F_{[1,5]} = 26.6$, $p = 0.004$; 1989: latitude $F_{[1,2]} = 0.1$, $p = 0.75$, locality type $F_{[1,2]} = 20.0$, $p = 0.045$; 1990: latitude $F_{[1,4]} = 21.5$, $p = 0.010$, locality type $F_{[1,4]} = 31.3$, $p = 0.005$.
T 4. ANCOVA, 1988: latitude $F_{[1,11]} = 1.0$, $p = 0.33$, locality type $F_{[1,11]} = 16.5$, $p = 0.002$; 1989: latitude $F_{[1,11]} = 3.7$, $p = 0.08$, locality type $F_{[1,11]} = 2.0$, $p = 0.19$; 1990: latitude $F_{[1,12]} = 1.0$, $p = 0.34$, locality type $F_{[1,12]} = 19.5$, $p = 0.001$.
T 5. ANOVA, $F_{[1,5]} = 0.2$, $p = 0.70$.
T 6. ANOVA, 1988: $F_{[1,7]} = 0.4$, $p = 0.57$; 1989: $F_{[1,4]} = 0.2$, $p = 0.66$; 1990: $F_{[1,7]} = 0.01$, $p = 0.90$.
T 7. ANOVA, $F_{[2,16]} = 0.2$, $p = 0.81$.
T 8. ANOVA, $F_{[1,16]} = 16.2$, $p = 0.001$.
T 9. Paired t-test, 1988: $t_7 = 1.2$, $p = 0.27$; 1989: $t_3 = 1.7$, $p = 0.19$; 1990: $t_6 = 0.6$, $p = 0.55$.
T 10. ANCOVA, year: $F_{[2,15]} = 0.8$, $p = 0.45$; locality type: $F_{[1,15]} = 1.2$, $p = 0.29$.
T 11. ANCOVA, year: $F_{[2,17]} = 0.6$, $p = 0.54$; latitude: $F_{[1,17]} = 1.3$, $p = 0.28$.
T 12. ANCOVA, year: $F_{[2,40]} = 0.8$, $p = 0.47$; latitude: $F_{[1,40]} = 11.9$, $p = 0.001$.
T 13. ANOVA, 1988: $F_{[1,13]} = 4.6$, $p = 0.05$; 1989: $F_{[1,12]} = 4.2$, $p = 0.06$; 1990: $F_{[1,13]} = 3.1$, $p = 0.10$.
T 14. Paired t-test, 1988: $t_8 = 3.2$, $p = 0.012$; 1989: $t_4 = 1.9$, $p = 0.14$; 1990: $t_6 = 1.4$, $p = 0.20$.
T 15. ANCOVA, 1988: latitude $F_{[1,11]} = 8.0$, $p = 0.016$, locality type $F_{[1,11]} = 20.9$, $p = 0.001$; 1989: latitude $F_{[1,10]} = 25.8$, $P < 0.001$; locality type $F_{[1,10]} = 11.2$, $p = 0.007$; 1990: latitude $F_{[1,10]} = 20.3$, $p = 0.001$, locality type $F_{[1,10]} = 9.9$, $p = 0.010$.
T 16. ANCOVA, 1988: latitude $F_{[1,9]} = 7.8$, $p = 0.021$, locality type $F_{[1,9]} = 0.5$, $p = 0.49$; 1989: latitude $F_{[1,5]} = 18.7$, $p = 0.008$; locality type $F_{[1,5]} = 0.1$, $p = 0.78$; 1990: latitude $F_{[1,8]} = 36.8$, $P < 0.001$, locality type $F_{[1,8]} = 0.3$, $p = 0.66$.
T 17. ANCOVA: latitude $F_{[1,6]} = 8.4$, $p = 0.027$, locality type $F_{[1,6]} = 0.02$, $p = 0.90$.
T 18. ANCOVA: latitude $F_{[1,9]} = 0.05$, $p = 0.84$; locality type $F_{[1,9]} = 9.6$, $p = 0.013$.
T 19. ANOVA, seasonal averages: $F_{[2,30]} = 0.5$, $p = 0.58$; average week 32: $F_{[2,21]} = 0.4$, $p = 0.70$; average week 34: $F_{[2,15]} = 1.8$, $p = 0.19$.
T 20. ANOVA, adults: $F_{[1,4]} = 0.05$, $p = 0.84$; juveniles: $F_{[1,24]} = 0.03$, $p = 0.86$.
T 21. ANCOVA, latitude: $F_{[1,2]} = 6.5$, $p = 0.12$; locality type: $F_{[1,2]} = 0.8$, $p = 0.46$.
T 22. ANCOVA, latitude: $F_{[1,3]} = 14.3$, $p = 0.033$; locality type: $F_{[1,3]} = 9.6$, $p = 0.05$.
T 23. ANCOVA, 1989: latitude, $F_{[1,10]} = 12.7$, $p = 0.005$; locality type, $F_{[1,10]} = 14.4$, $p = 0.003$; 1990: latitude, $F_{[1,11]} = 2.4$, $p = 0.15$, locality type, $F_{[1,11]} = 13.0$, $p = 0.004$.
T 24. ANCOVA, 1989: latitude, $F_{[1,5]} = 0.001$, $p = 0.98$; locality type, $F_{[1,5]} = 0.1$, $p = 0.78$; 1990: latitude, $F_{[1,6]} = 0.2$, $p = 0.67$, locality type, $F_{[1,6]} = 0.7$, $p = 0.18$.
T 25. ANCOVA: latitude, $F_{[1,4]} = 0.6$, $p = 0.47$; locality type, $F_{[1,4]} = 89.1$, $p = 0.001$.
T 26. ANOVA, $F_{[1,3]} = 1.0$, $p = 0.39$.
T 27. Paired t-test, 1989: $t_4 = 4.8$, $p = 0.009$, 1990: $t_2 = 4.0$, $p = 0.058$.
T 28. ANCOVA, males 1988: latitude, $F_{[1,12]} = 0.1$, $p = 0.71$; locality type, $F_{[1,12]} = 1.7$, $p = 0.22$; males 1989: latitude, $F_{[1,10]} = 10.8$, $p = 0.008$, locality type, $F_{[1,10]} = 1.1$, $p = 0.32$; males 1990: latitude, $F_{[1,12]} = 3.0$, $p = 0.11$, locality type, $F_{[1,12]} = 3.1$, $p = 0.10$; females 1988: latitude, $F_{[1,12]} = 0.1$, $p = 0.79$; locality type, $F_{[1,12]} = 3.4$, $p = 0.09$; females 1989: latitude, $F_{[1,11]} = 3.3$, $p = 0.10$, locality type, $F_{[1,11]} = 1.2$, $p = 0.31$; females 1990: latitude, $F_{[1,12]} = 1.3$, $p = 0.27$, locality type, $F_{[1,12]} = 0.8$, $p = 0.39$.
T 29. ANOVA, males 1990, moult score >5: $F_{[1,3]} = 8.2$, $p = 0.06$; females 1988, moult score >3: $F_{[1,3]} = 21.8$, $p = 0.019$; moult score >5: $F_{[1,4]} = 1.8$, $p = 0.25$; females 1989, moult score >3: $F_{[1,3]} = 39.4$, $p = 0.008$; females 1990, moult score >5: $F_{[1,4]} = 13.0$, $p = 0.023$.
T 30. Spearman rank correlation, 1988: $r_s = 0.928$, $n = 6$, $p<0.05$, 1989: Spearman rank correlation, $r_s = 0.986$, $n = 6$, $p<0.05$, 1990: Spearman rank correlation, $r_s = 0.928$, $n = 7$, $p<0.01$.

Appendix 3

Suggestions for further analyses *Förslag till vidare analyser*

Many interesting analyses were not possible to carry out in the present study due to how data were compiled and reported. Below we suggest some analyses that can be carried out by bird observatories and ringers using data from one site only. Irrespective of whether such analyses will support or reject the conclusions drawn in the present study, they will add to our knowledge about the migration performance of Willow Warblers. Your contribution is important !

Många intressanta analyser kunde inte genomföras på grund av det sätt materialet sammanställdes på. Nedan föreslår vi därför ett antal analyser som fågelstationer och enskilda ringmärkare kan göra på sina egna material. Oavsett om sådana analyser kommer att stödja eller förkasta de slutsatser som dragits i den här studien, så kommer de att bli viktiga bidrag till vår gemensamma kunskap om lövsångarens flyttning genom Sverige. Ditt bidrag är lika viktigt som något annat !

- The proportion of juveniles was higher than expected for the population at most sites. Analyse how the age proportions varies over time (days, weeks, months) in relation to weather variables, moult and time of season.
  Proportionen ungfåglar var oförklarligt hög på många lokaler. Varför ? Slå ihop materialet över lämpliga tidsintervall (dagar, veckor, månader) och undersök hur proportionen ungfåglar varierar i förhållande till väder (med- respektive motvind, dimma eller regn respektive god sikt), ruggning (påverkas åldersproportionen av var i ruggningen fåglarna befinner sig ?) och tid på säsongen (har åldersgrupperna olika sträckperioder ?).
- To few adults were scored for fat to allow a comparison with juveniles. But with data from several years it should be possible. Which birds do normally carry the largest fat deposits at your site, adults or juveniles ? Does it vary with season and state of moult ? Which sex carries most fat ?
  Alltför få adulter fångades för att tillåta en jämförelse av fettreserverna hos adulter och ungfåglar. Med flera års data tillgängliga bör en sådan jämförelse vara möjlig. Vilken ålderskategori är fetast på din lokal ? Varierar det med tid på säsongen eller med ruggningsstatus ? Är hanarna eller honorna fetast ?
- In the period when juveniles had an average moult score of 5 or more, they were generally fatter than in the period of moult score 3. A more direct way to show if older birds carry more fat is to look at the individual level. What is the average fat score of juveniles in different moult scores at your site?
  Under den period när ungfåglarna i genomsnitt var i ruggningsstadie 5 var de överlag fetare än i ruggningstadie 3. Ett mer direkt sätt att testa huruvida fåglarna verkligen är fetare mot ruggningens slut är att använda data på individnivå. Vilken är den genomsnittliga fettnivån för ungfåglar i de olika ruggningsstadierna vid din lokal?
- It seems as if Willow Warblers rarely become very fat during autumn in Sweden. But again, more data than from three years may be necessary. What proportion of individuals in fat score 6 are trapped at your site ? Are there differences between age classes and sexes ?
  Det verkar som att ytterligt få lövsångare i Sverige på hösten blir riktigt feta (fettklass 6). Men för de flesta platser behövs ett större material än från tre år för att säkra slutsatser skall kunna dras. Hur stor andel av lövsångarna på din lokal är riktigt feta ? Är mönstret olika för de olika könen och åldersklasserna ?
- Changes in fat score and body mass of retraps give important information on whether and when significant fattening occurs at a site. But again, at most sites more than three study years are probably necessary to collect enough data. Looking at retraps from all study years at your site, is there a pattern emerging ? Are there differences between age classes and sexes ?
  Förändringar i fettklass och kroppsmassa hos återfångade fåglar ger viktig information om huruvida betydande fettupplagring äger rum på en plats. På de flesta platser behövs det dock data från mer än tre år för att slutsatser skall kunna dras. Alla undersökningsår sammantaget, hur många av lövsångarna på din lokal lägger på sig stora mängder fett ? Är mönstret olika för de olika könen och åldersklasserna ?

Sammanfattning

Lövsångarens Phylloscopus trochilus *höstflyttning genom Sverige: resultat från ett landsomfattande samarbetsprojekt*

I Sverige är lövsångaren företrädd av två raser: i Götaland och Svealand häckar *Phylloscopus trochilus trochilus* och i Norrland häckar *Ph. t. acredula.* Den sydliga rasen flyttar mot sydväst till övervintringskvarter i västra Afrika och den nordliga rasen flyttar mot sydsydost till vinterkvarter i centrala och sydöstra Afrika. Tidigare har artens höstflyttning och ruggning studerats vid några få platser i landet, men för att få en helhetsbild av höststräckets förlopp genom Sverige krävdes en större och samordnad insats. I den här artikeln redovisar vi resultat från ett rikstäckande projekt där fågelstationer och ringmärkare samtidigt samlat in data på lövsångare enligt standardiserade metoder. Projektet syftade till att: 1) samla in ett stort datamaterial för en flyttfågel i Sverige, 2) att uppmuntra målinriktade studier bland fågelstationer och ringmärkare och 3) att förstärka samarbetet mellan svenska fågelstationer. Ett viktigt led i projektet var att stationerna själva skulle engagera sig i databearbetningen.

Material och metoder

För varje fångstplats rapporterades antal fångstdagar per säsong, första fångstdag samt fångstintensitet (se Appendix 1). Fåglarna åldersbestämdes till juvenila eller adulta (1K respektive 2K+) och vinglängd registrerades till närmaste mm. Mängden fett klassificerades enligt en skala 0–6, där 0 innebär inget synligt fett under huden och 6 innebär stora fettdepåer. Fåglarnas kroppsvikt registrerades till närmaste 0.1 g. En skala (1–6) användes för att registrera framskridandet av ungfåglarnas kroppsfjäderruggning, där ruggningsstadium är ungefärligt relaterat till fågelns ålder enligt: 1 = 21 dagar, 2 = 27 d, 3 = 32 d, 4 = 37 d, 5 = 44 d och 6 > 60 d.

Stationerna rapporterade medianfångstdatum för adulta och juvenila lövsångare, proportionen återfångade fåglar samt proportionen av dem som ökat med mer än två fettklasser, eller med mer än 1 g i vikt, sedan märktillfället. Könsbestämning gjordes med hjälp av vinglängd enligt kriterierna: adult hane > 68 mm, adult hona < 67 mm, ung hane > 67 mm, och ung hona < 66 mm. Vi har endast inkluderat data i en analys om medelvärdet bygger på ett stickprov om åtminstone 30 fåglar och analyser av säsongsmässiga trender gjordes bara på material där minst 30 fåglar fångats per vecka under minst sex veckor i följd.

Materialet har analyserats genom ett stort antal statistiska tester. För att inte belasta den löpande texten med alltför mycket detaljer om dessa tester har värden av testvariabler, frihetsgrader och signifikansnivåer sammanställts i Appendix 2, med hänvisningar till dessa i den engelska texten.

Resultat

Totalt skickades data in från 18 fågelstationer och fångstplatser som sammanlagt fångade över 36 000 lövsångare inom ramen för projektet under höstarna 1988–1990 (Tabell 1, Fig. 1). Flera stationer som anmält sitt intresse skickade dock aldrig in data (även om sådana hade samlats in). Fångstplatserna klassificerades i efterhand som antingen kust- eller inlandslokaler (Tabell 1).

Proportionen ungfåglar varierade mellan 67% och 99% mellan platser och år (Tabell 1). Det fanns inget samband mellan proportionen ungfåglar och latitud eller fångstplatstyp (kust- eller inlandslokal). Proportionen ungfåglar minskade normalt något över säsongen på respektive lokaler.

Lövsångare fångades inte senare på hösten vid sydliga än vid nordliga platser. Däremot fångades juvenila fåglar ungefär två veckor tidigare vid inlandslokaler än vid kustlokaler. Det fanns ingen könsskillnad i medianfångstdatum, men vid kustlokaler fångades ungfåglar i genomsnitt några dagar före gamla fåglar.

Ungfåglarna hade i genomsnitt längre vingar ju längre norrut de fångades (Tabell 2), men hos adulta fåglar var detta samband inte signifikant. Vinglängden ökade successivt under hösten på en och samma lokal (Fig. 2), förmodligen i samband med att inslaget av fåglar med ett nordligare ursprung ökade. De adulta fåglarna hade i genomsnitt längre vinge än ungfåglarna (Tabell 2).

I genomsnitt var kroppsfjäderruggningen hos ungfåglarna mer framskriden ju längre söderut i Sverige fåglarna var fångade och den var längre kommen vid kustlokaler jämfört med inlandslokaler (Tabell 3, Fig. 3). Eftersom fångstperioden skiljer sig från söder till norr jämförde vi ruggningsstadium under två givna veckor, vecka 32 (runt 10 augusti) och vecka 34 (runt 24 augusti). Under vecka 32 var ruggningen mer framskriden i söder än i norr, men skilde sig inte mellan kust och inland. Under vecka 34 var mönstret i stort sett detsamma som under vecka 32, men 1988 hade fåglarna vid kusten kommit längre i ruggningen än de i inlandet.

I södra Sverige var de adulta fåglarna i genomsnitt fetare än ungfåglarna, medan det inte fanns någon skillnad mellan åldersklasserna i norra Sverige (Tabell 4). Hos ungfåglar som nått ruggningsstadium 3 (32 dagars ålder) hade mängden fett inget samband med latitud eller typ av lokal (kust eller inland). Vid ruggningsstadium 5 (44 dagars ålder) var fåglarna betydligt fetare än i ruggningsstadium 3 och fåglarna vid kusten var fetare än de i inlandet (Tabell 5, Fig. 4).

På respektive lokal ökade mängden fett i genomsnitt över säsongen hos ungfåglar, medan alltför få adulta fåglar fångades för att tillåta en meningsfull analys. Andelen riktigt feta fåglar (fettklass 6) var generellt låg (Tabell 6). I genomsnitt var 8.5% (1989) och 2.4% (1990) riktigt feta hos adulta fåglar och 3.0% (1989) och 2.6% (1990) hos juvenila fåglar. Den högsta andelen feta fåglar registrerades vid Falsterbo, där 22.6% av de adulta och 7.1% av de juvenila lövsångarna hade fettklass 6. Proportionen fåglar som ökade tre fettklasser mellan fångst och återfångst var mellan 2% och 5% för båda ålderskategorierna (Tabell 7).

Genomsnittliga vikter redovisas i Tabell 8 och vikter i olika ruggningsstadier hos ungfåglar redovisas i Tabell 9. Adulta fåglar var något tyngre än juvenila fåglar och hanar var tyngre än honor. Bland juvenila fåglar tenderade den genomsnittliga vikten att minska från norr till söder, men det var ingen skillnad i vikterna mellan kust- och inlandslokaler. I kontrast mot fettklass så fanns ingen säsongsmässig ökning i vikterna hos ungfåglar studerade på samma lokal. Proportionen fåglar som ökade i vikt med mer än 1.0 g mellan fångst och återfångst var endast 2–5% för både adulta och juvenila fåglar (Tabell 10).

Diskussion

Andelen ungfåglar i fångsten var mycket hög både vid kust- och inlandslokaler (93%), vilket troligen inte representerar den verkliga proportionen ungfåglar i populationen på hösten (som borde vara 70–75%). Det är ett välkänt faktum att vid fågelstationer fångas normalt en högre andel ungfåglar än man borde förvänta sig. I samband med frontpassager eller oförutsedda väderomslag kan man dock ibland fånga en mycket lägre andel ungfåglar, som troligen bättre motsvarar den sanna andelen bland den överflygande populationen. Även vid inlandslokalerna var andelen ungfåglar högre än man skulle ha förväntat sig, vilket troligen kan förklaras av att ungfåglar uppvisar spridningsrörelser innan den egentliga flyttningen och de är då lätta att fånga. Adulta fåglar däremot genomgår en komplett ruggning under samma period och är då mycket orörliga och undgår därför att bli fångade i samma utsträckning som ungfåglarna. Det finns även den möjligheten att inlandslokalerna som ingick i projektet utgjordes av "ekologiska öar" och därför inte är representativa som typiska rastlokaler för lövsångare. Ytterligare en möjlighet till att andelen adulta fåglar är så låg i fångsten är att dessa genom större fettdepåer och spetsigare vingar genomför längre flygetapper än ungfåglarna och således inte rastar lika många gånger i Sverige.

Ungfåglarna passerade fångstplatserna i genomsnitt något före de adulta, en effekt som troligen uppstår på grund av den mer tidskrävande kompletta ruggningen hos adulter. Däremot fanns ingen tidsskillnad i flyttningen mellan könen. Genom att använda ruggningsskalan för åldersbestämning av ungfåglar kunde vi visa att ungfåglar med nordligt ursprung, av rasen *acredula*, ger sig iväg på sin första höstflyttning vid en lägre ålder (de är ungefär två veckor yngre) än de sydliga *trochilus*.

Generellt hade ungfåglarna kommit längre i sin ruggning när de fångades på kustlokalerna, vilket förmodligen återspeglar att dessa fåglar verkligen gett sig iväg på flyttning. Fåglarna på inlandslokalerna utgörs till en del av fåglar som befinner sig i spridningsfasen (se nedan) och som ännu inte startat den egentliga flyttningen. Det fanns ett negativt samband mellan latitud och ruggningsstadium hos ungfåglarna, vilket sannolikt återspeglar den tidigare häckningen i söder.

Det visade sig vid flera lokaler att den genomsnittliga fettklassen ökade under säsongen, medan vikten höll sig konstant under samma period (Fig. 5). Detta beror sannolikt på att mängden vatten som en fågel bär är större under ruggningen. När ruggningen lider mot sitt slut minskar mängden vatten i kroppen, samtidigt som mängden fett ökar. Även om totalvikten inte ökat så har fågelns flyttningsberedskap drastiskt ändrats. Fettklass är därför sannolikt det som bäst karaktäriserar fåglarnas energidepåer och den följande diskussionen grundar sig på fettdata.

Vi fann indikationer på att adulta fåglar hade större fettreserver än ungfåglar i södra Sverige. Att adulta fåglar har större energireserver än ungfåglar under flyttningen är det mönster man normalt finner hos andra arter. Under första hälften av kroppsfjäderruggningen hade ungfåglarna mycket små fettreserver. Detta kan bero på åtminstone ett par olika faktorer. Under den perioden rör sig fåglarna kortare sträckor, troligen för att lära känna sitt hemområde inför kommande säsonger och/eller för att lära sig hitta tillbaka nästa år. Dessa förflyttningar är troligen korta och inga stora energireserver krävs. Alternativt så tillåter fåglarnas energibudget inte någon kraftig fettackumulering samtidigt med den energikrävande ruggningen och fåglarna kan inte öka sina fettreserver. Mot slutet av kroppsruggningen ökade fettreserverna emellertid och detta återspeglar förberedelserna för den verkliga flyttningen. Det faktum att fåglar fångade vid kustlokaler hade större fettreserver speglar att vi här har att göra med fåglar som verkligen är på flyttning i större utsträckning än vid inlandslokalerna. I jämförelse med en del andra arter, som till exempel rörsångare *Acrocephalus scirpaceus* och sävsångare *A. schoenobaenus*, har lövsångaren förhållandevis små fettreserver när de flyttar bort på hösten. Detta indikerar att flyttningen sker i korta flygetapper. Det är emellertid känt att lövsångare som står inför passagen av t ex Sahara har betydligt större fettdepåer än dem vi fann i Sverige på hösten.

Slutligen menar vi att "lövsångarprojektet" varit mycket lyckat och att en hel del ny information om artens flyttning kommit fram tack vare den samordnade insatsen bland svenska fågelstationer och ringmärkare. Även om det fortfarande återstår mycket att klarlägga vad gäller lövsångarens flyttning (se Appendix 3), hoppas vi att deltagarna är tillfreds med resultatet och att "lövsångarprojektet" skall inspirera till liknande projekt i framtiden.