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Fuel deposition and potential flight ranges of Blackcaps *Sylvia atricapilla* and Whitethroats *Sylvia communis* on spring migration in The Gambia

CHRISTIAN HJORT, JAN PETTERSSON, ÅKE LINDSTRÖM & J. MICHAEL B. KING

Abstract

Spring migration of Palaearctic passerines was studied on Ginak Island in The Gambia, as part of the European Science Foundation network "Palaearctic-African Songbird Migration". In this paper data collected from Blackcaps *Sylvia atricapilla* and Whitethroats *Sylvia communis*, which in late March-early April prepare for the crossing of the Sahara desert, are analysed. On a diet of mainly *Maytenus senegalensis* berries these warblers put on up to 3–4 % body mass per day and when ready for take off 35–40 % of their mass consists of fuel for the trip. According to conventional flight-range calculations this gives them flight ranges in still air of maximum 1200 km, which will not take them unaided across the desert. But predictable tailwinds, usually found at altitudes above c. 2500 m, may help them to central Morocco or beyond. In addition,

recent wind-tunnel experiments have suggested a distinctly reduced drag coefficient for use in the flight-range calculations, and this may extend the still-air range to more than 2500 km. In that case the desert crossing would be possible also without the help of tailwinds.

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The main hazard for spring migrating palaeartic birds wintering in tropical Africa is the crossing of the Sahara desert (e.g. Moreau 1972) where, with the exception of a few scattered oases (e.g. Ash 1969, Bairlein 1988, 1992), water and food is in principle unavailable for 1500–2000 km. How the birds, at the height of the dry season south of the desert, prepare for and thereafter carry out this passage has for long interested ornithologists, and through the years a number of studies have been carried out (e.g. Ash 1969, Fry *et al.* 1970, Dowsett & Fry 1971, Stoate & Moreby 1995, and the overview of the question by Moreau 1972). This problem is also central in the network program "Spatio-temporal course, ecology and energetics of Western Palaearctic-African songbird migration", organized by the European Science Foundation (Bairlein 1993).

As part of the ESF- program trapping and ringing of palaeartic migrants have been carried out on Ginak Island in The Gambia, West Africa, during the springs of 1995 and 1996, organized by J.M.B. King. The scope of this paper is to describe and discuss the

pre-migratory fuel-deposition in Blackcaps *Sylvia atricapilla* and Whitethroats *Sylvia communis*, based on data from 1995.

Working area and methods

Ginak Island (Fig. 1) is a 2–4 km wide and 10 km long coastal spit, stretching northwards from the mouth of the Gambia River. Its northern end reaches into Senegal. The vegetation is a coastal variety of Guinea savanna, with a fringe of mangrove on the inland side.

Our work was based on the Madiyana Lodge, situated close to the Senegalese border, among largely inactive sand dunes covered with scrubby *Acacia* woodland, with Tamarisk scrub in the moister depressions between the dunes. The shrub *Maytenus senegalensis* was common and its fruits constituted a major part of the diet of the palaeartic migrants, including the two species discussed here.

In 1995 work started 3 March and ended 6 April. The trapping was carried out within a few hundred

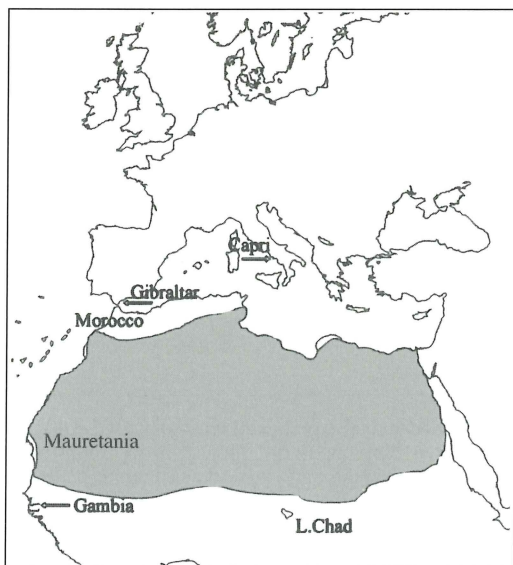


Fig. 1. Map of Africa and the western Palearctic, with the Sahara desert shaded

Afrika och västra Palearktis, med Sahara skuggat

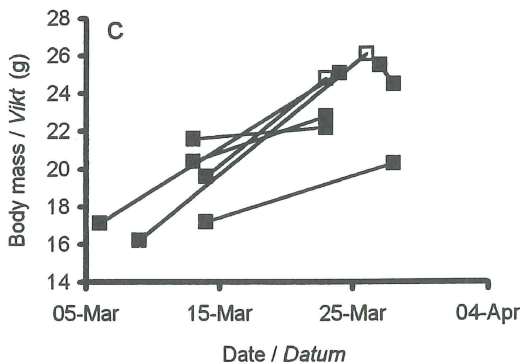
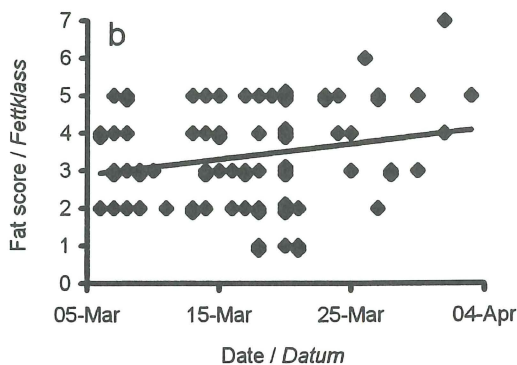
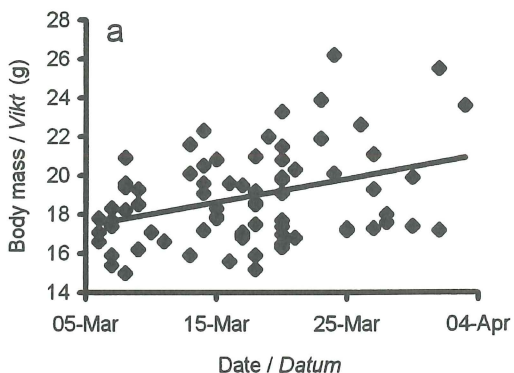
meters of the lodge, both in Acacia woodland and Tamarisk scrub, using a maximum of 12 60' (18 m) mist-nets. The nets were used every day from before dawn to about 11 am, and sometimes also for about 3 hours before sunset. Between 3–5 persons were involved at the same time and the grand total of

Fig. 2. (a) Body mass measurements in relation to trapping date and the general mass gain trend ($y=0.12x + 16.78$, $r^2=0.12$, $p=0.002$, $n=77$) for Blackcaps during spring 1995. (b) Fat-score measurements in relation to trapping date and the general fattening trend ($y=0.04x + 2.69$, $r^2=0.05$, $p=0.059$, $n=78$) for Blackcaps during spring 1995. (c) Retraps, showing body mass changes in individual Blackcaps during spring 1995. Filled squares represent birds trapped in the morning, open squares corrected values (see text) for birds trapped in the afternoon.

(a) Vikt i förhållande till fångstdatum hos svarthättor våren 1995, samt regressionslinjen och den statistiska signifikansen för sambandet mellan vikt och datum. (b) Fettklass i förhållande till fångstdatum hos svarthättor våren 1995, samt regressionslinjen för sambandet mellan fettklass och datum. (c) Viktutvecklingen hos svarthättor som kontrollerades en tid efter ringmärkningen våren 1995. Fyllda symboler visar vikter från fåglar fångade på morgonen, öppna symboler korrigerade kvällsvikter (se texten).

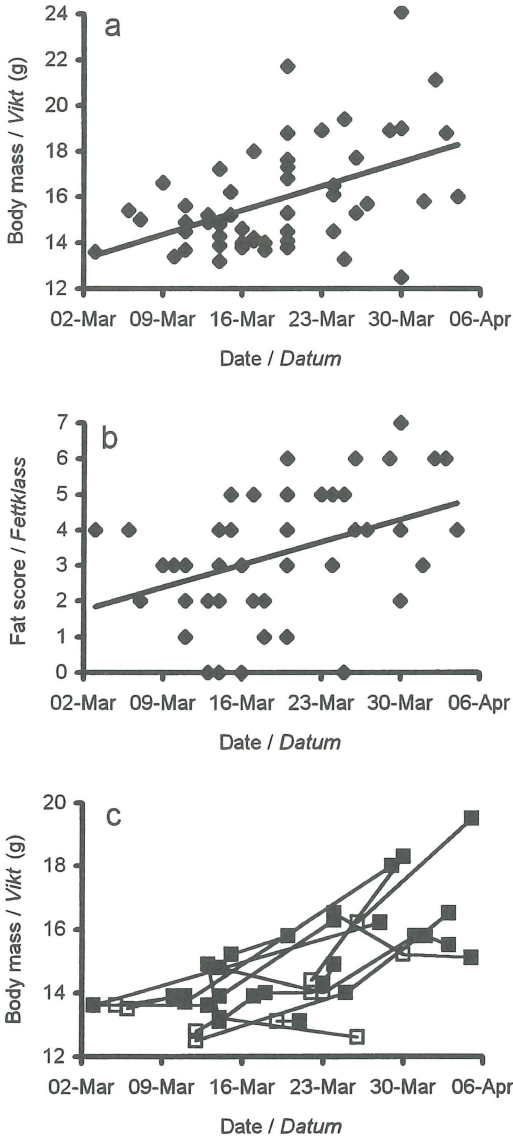
palearctic migrants ringed was 278, representing 17 species. Among these were 87 Blackcaps and 73 Whitethroats.

The birds were weighed with a Pesola balance and visible fat was scored using the 8 class (0–7) scale of Kaiser (1993). Ageing and sexing was done according to Svensson (1992) and Jenni & Winkler (1994), wing length measured according to the maximum method (method 3) of Svensson (1992).



Results

Of the Blackcaps all birds were sexed (62% males) and 77 (89%) aged (10% ad.). Of the Whitethroats 32 birds (44%) were sexed (61% males), almost all of them after 24 March, and 65 (89%) were aged (20% ad.). Of the total of 87 Blackcaps and 73 Whitethroats trapped, 7 (8%) and 18 (25%) respectively were retrapped one or more times.



The distribution over time of body mass and fat score, and the body mass development of individual retrapped birds, are shown in Fig. 2 for the Blackcap, and in Fig. 3 for the Whitethroat. Birds which were originally trapped in the afternoon (8 Blackcaps and 18 Whitethroats) are excluded from all analyses of body mass and fat scores – except for the analyses of retraps, where a correction for the time of day has been applied.

Body mass and fat scores in relation to trapping date

In the Blackcap body mass increased significantly with date of trapping, but the relationship between date and the more open ended fat score was not fully significant (Fig. 2). Body mass, but not fat score, was significantly higher in the second half of the study period (after 20 March) than in the first: body mass 20.0 ± 3.0 (SD) g vs. 18.5 ± 2.1 g, fat score 3.9 ± 1.6 vs. 3.2 ± 1.8 (body mass, $t_{75}=2.4$, $p=0.02$; fat score, $t_{76}=1.9$, $p=0.067$). There were no effects of either age or sex on the relationship between body mass and fat score, respectively, and date (ANCOVA, effect of age on body mass $F_{[1,65]}=0.1$, $p=0.70$, on fat score $F_{[1,65]}=0.1$, $p=0.74$; effect of sex on body mass $F_{[1,73]}=0.2$, $p=0.64$, on fat score $F_{[1,73]}=0.4$, $p=0.52$).

In the Whitethroat both body mass and fat score increased significantly with date (Fig. 3). Birds were significantly heavier and fatter after 20 March than before: body mass 17.3 ± 2.9 (SD) g vs. 15.2 ± 1.8 g, fat score 4.3 ± 1.8 vs. 2.8 ± 1.6 (body mass, $t_{53}=3.3$, $p=0.002$; fat score $t_{53}=3.0$, $p=0.004$). As in the Black-

Fig. 3. (a) Body mass measurements in relation to trapping date and the general mass gain trend ($y=0.15x + 13.00$, $r^2=0.24$, $p<0.001$, $n=55$) for Whitethroats during spring 1995. (b) Fat-score measurements in relation to trapping date and the general fattening trend ($y=0.09x + 1.58$, $r^2=0.15$, $p=0.003$, $n=55$) for Whitethroats during spring 1995. (c) Retraps, showing body mass changes in individual Whitethroats during spring 1995. Filled squares represent birds trapped in the morning, open squares corrected values (see text) for birds trapped in the afternoon.

(a) Vikt i förhållande till fångstdatum hos törnsångare våren 1995, samt regressionslinjen och den statistiska signifikansen för sambandet mellan vikt och datum. (b) Fettklass i förhållande till fångstdatum hos törnsångare våren 1995, samt regressionslinjen för sambandet mellan fettklass och datum. (c) Viktutvecklingen hos törnsångare som kontrollerades en tid efter ringmärkningen våren 1995. Fyllda symboler visar vikter från fåglar fångade på morgonen, öppna symboler korrekterade kvällsvikter (se texten).

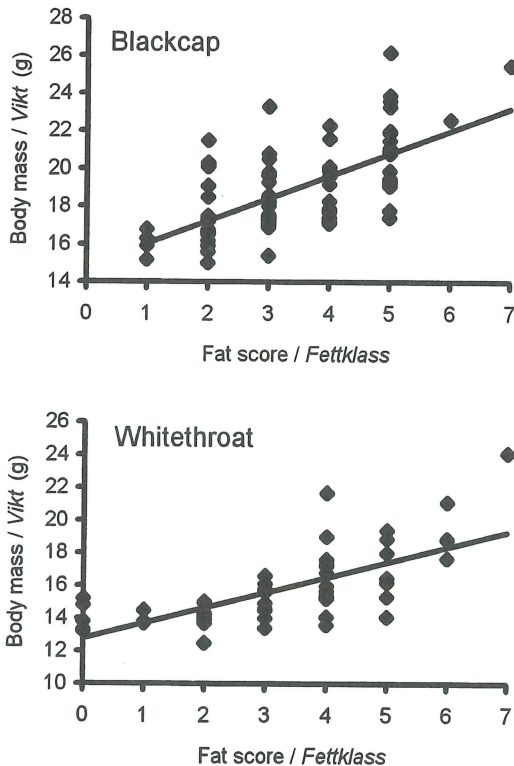


Fig. 4. (a) The body mass / fat score relationship ($y=1.20x + 14.83$, $r^2=0.43$, $p<0.01$, $n=77$) in Blackcaps. (b) The body mass / fat score relationship ($y=0.93x + 12.76$, $r^2=0.50$, $p<0.01$, $n=55$) in Whitethroats.

(a) Relationen mellan vikt och fettklass hos svarthätta. (b) Relationen mellan vikt och fettklass hos törnsångare.

cap there was no effect of age on the relationship between body mass and fat score, respectively, and date (ANCOVA, effect of age on body mass, $F_{[1,44]}=0.02$, $p=0.90$, on fat score $F_{[1,44]}=0.6$, $p=0.45$). Too few birds were sexed to test any corresponding effect of sex on body mass and fat score.

Body mass and fat score relationships

For both species the relationship between body mass and fat score was highly significant (Fig. 4). Including all trapping occasions, Blackcap body masses in 1995 varied between 15.0 and 27.6 g and fat scores between 1 and 7. The corresponding figures for the Whitethroat were 12.5–24.1 g and 0–7.

Retraps

Six out of seven retrapped Blackcaps increased in mass (Fig. 2c). Two of these were first trapped in the morning and retrapped in the afternoon. To compensate for the within-day mass increase we subtracted 1.5 g from the afternoon weights of these two birds. The other birds were both ringed and retrapped in mornings or evenings, respectively. The average mass increase was 0.4 g/day (on average 4.9 g over an average period of 13 days, $n=6$). Assuming a lean body mass of 15 g (the mean of 11 fat-score 0 Blackcaps weighed in early spring 1996 was 15.4 g), the average rate of mass increase was 2.4% of lean mass/day (1996 values are used in this particular case as, due to the later start of ringing in 1995, there were no 0 measurements for Blackcaps that year, and very few for Whitethroats). The two highest rates of increase (corrected values) were 9.9 g in 17 days and 5.2 g in 9 days. For both these birds the average mass increase was 0.6 g/day, corresponding to 3.5% of lean mass/day.

Many Whitethroats were ringed in the morning and retrapped in the afternoon, or vice versa (Fig. 3c). To make the body mass values comparable we subtracted 1.2 g from all afternoon weights, assuming this to be a reasonable within-day mass increase. Several birds were retrapped more than once (up to three times). Fifteen out of 18 retrapped birds had increased in mass when retrapped the last time. If retrapped more than once, we included only the occasions when mass increased up to the last trapping. The average mass increase for the Whitethroats was 0.2 g/day (on average 1.7 g over an average period of 9 days, $n=15$). Assuming a lean body mass of 12 g (the mean of 15 fat score 0 Whitethroats weighed in early spring 1996 was 12.2 g.; 1996 values used here, as for the Blackcap, see explanation above), the average rate of mass increase was 1.7 % of lean mass/day. The two highest increases were 3.9 g in 8 days (0.5 g/day or 4.1% of lean body mass/day) and 0.9 g in 2 days (0.5 g/day and 3.8% of lean mass/day).

Discussion

Different starting areas?

The fuel deposition patterns of the two species, as indicated by the retraps, seem slightly different. Five out of 7 retrapped Blackcaps showed distinct increases in mass (Fig. 2 c), and the other two remained at the same level (one of these in the maximum fat score class 7, when retrapped after only one

day). In contrast 4 out of 18 Whitethroats started with losing fat and mass (Fig. 3c). This indicates that many Whitethroats trapped by us may just have arrived from further south in Africa (cf. Mehlum 1983, Hansson & Pettersson 1989). A similar conclusion was drawn by Fry *et al.* (1970) for weight-losing Whitethroats at Lake Chad. Thus most of the Blackcaps trapped by us may have wintered in The Gambia – or moved into the area earlier in the season – whereas many of the Whitethroats may have been transients.

The gradual northward exodus of both species around the shift from March to April is indicated by the decreasing numbers of birds trapped (Figs. 2a and 3a), with trapping efforts remaining largely constant.

Fuelling rates and flight ranges

In the Blackcap, an increase with one fat-score class means an average body mass increase of about 1 g (Fig. 4a). The calculated average mass increase was 0.4 g/day (maximum 0.6 g/day) and the average rate of mass increase 2.4%/day (maximum 3.5%/day). The latter figure is only one third of the maximum fat deposition rate given for the Blackcap by Langslow (1976; see also Lindström 1991, fig. 3).

An increase from fat score 0 to 6 means that a Blackcap accumulates about 7 g fuel and an increase to class 7 about 8 g. In the latter case c. 35% of the body mass in birds ready for take-off consists of fuel for the trip.

A fat score class 7 Blackcap may weigh as much as 25 g and a class 0 bird 15 g. Using Pennycuick's calculation manual (Pennycuick 1989, program 1, version 1:1, 1992 update), with a measured average wingspan value of 20 cm (n=5) and with an approximate small bird aspect ratio of 4.8, such a class 7 Blackcap should have a flight range in still air of c. 1600 km. If we also consider that only c. 70% of the fuel load is fat, the rest being less energy rich protein (Klaassen & Biebach 1994), this range may have to be reduced to c. 75%, which corresponds to a flight range of 1200 km. In still air this will not bring the bird to refuelling areas in Morocco, only to the barren wastes of northern Mauretania.

In the slightly smaller Whitethroat, an increase with one fat-score class means a weight increase of about 0.85 g (Fig. 4b). The calculated average mass increase was 0.2 g/day (maximum 0.5 g/day) and the average rate of mass increase 1.7%/day (maximum c. 4%/day).

A fat-score class 7 Whitethroat may weigh 20 g

and carries 7–8 g more fuel than the class 0 bird. This means that for these birds c. 40 % of their body mass is fuel. Using the same rough way of calculating flight ranges as for the Blackcaps (with a measured average wingspan value of 20 cm (n=4) and the aspect ratio 4.8, a decrease from class 7 to class 0 from 20 – 12 g (Fig. 4b) and a reduction of the calculated range to 75% (due to fat vs. protein mobilization rates), we find that under still air conditions a class 7 Whitethroat, like the Blackcaps, would only be able to travel c. 1200 km – which is not sufficient for the desert crossing.

The above calculations would thus seemingly lead to the conclusion that these warblers cannot manage the desert crossing without either refuelling en route, or using tailwinds.

As to the refuelling, Bairlein (e.g. 1988, 1992) showed that some migrants do refuel in the few and scattered Saharan oases. But the limited number of such places and the somewhat limited numbers of birds encountered there indicates that this is not the strategy adopted by the bulk of migrants.

As to the tailwinds, Biebach (1992), after calculating flight-ranges for autumn migrants trapped in the Mediterranean area and at desert sites south thereof (using Rayner's (1990) formula), came to the conclusion that they could not make the crossing without the aid of tailwinds. He also noted that in autumn the wind regimes normally allow the birds to profit from tailwinds. Piersma & van de Sant (1992), studying West African spring wind patterns in relation to wader migration, noted that birds which fly high (usually above 2500 m) and which adapt their flight altitude to the best winds, can profit from tailwinds of on average 15 km/h. If we put the Blackcap's and Whitethroat's air speed at 30–35 km/h (e.g. Alerstam 1990, Biebach 1992) that tailwind means a range extension of 40–50%. That should get the birds into viable refuelling areas in Morocco.

However, very recent wind-tunnel experiments (Pennycuick *et al.* 1996) have indicated that the drag coefficient hitherto used in the flight range calculations (Pennycuick 1989, and 1992 upgrade) has been grossly overestimated. It may indeed be only about 10% of what was earlier believed. If the new empirically derived coefficient is used, the still air flight ranges for both the Blackcap and Whitethroat will exceed 2500 km – which is more than needed to cross the Sahara without tailwinds!

Different populations with different timing?

When comparing our material with other spring migration data sets from sub-Saharan Africa we can, for the better studied Whitethroat, note that weights for April–May in Ethiopia (means 15–16 g, ranges between 11.3–22.1 g; Ash 1994) were largely similar to ours from The Gambia (Fig. 4b). The large Whitethroat material collected at Lake Chad in 1967–68 (Fry *et al.* 1970, Dowsett & Fry 1971) showed similar spring weights (mean 15.8, range 12.0–23.5 g). The latter study, as already mentioned, also found that retrapped Whitethroats at Lake Chad had a tendency to initially loose weight, indicating (as for our birds) arrival to a stopover site after migration from the south. But whereas the Whitethroats in The Gambia seem to have their maximum fat deposition and take-off period in late March–early April, the Lake Chad birds reached that period first about one month later, at the end of April and in early May. The mean fat deposition rate at Lake Chad was 0.6 g/day (Fry *et al.* 1970, p. 69), which is higher than our maximum rate from The Gambia. The later fattening and take-off probably indicates a more northerly, later available goal for Lake Chad birds than for the Whitethroats passing through The Gambia.

That the Whitethroats passing through The Gambia aim for more southerly breeding areas than those at Lake Chad is also indicated by the generally small wing lengths of the birds trapped in The Gambia (second year males 71.5 mm, n=12; second year females 71.3 mm, n=11; after second year males 70.3 mm, n=9; after second year females 72.3 mm, n=3). No wing lengths were given for the birds studied by Fry *et al.* (1970) at Lake Chad, but according to the recovery map in Glutz von Blotzheim & Bauer (1991, p. 859) they may be the same birds which en route northwards pass Capri in Italy in early May. These have on average 2–3 mm longer wings (Pettersson *et al.* 1990) than the Gambian birds.

The above conclusion is further substantiated by winter recoveries of British Whitethroats in Senegal (da Prato & da Prato 1983) and by the fact that in spring British birds arrive to their breeding areas some 3 weeks earlier than Swedish Whitethroats (Fransson 1995).

From a study at a spring stopover site in a southern Moroccan oasis, of birds which had covered most of the desert passage, Ash (1969) reported a mean mass for Blackcaps of 14.1 g. Using our data, this means a mean fat-score class around 0. The mean mass for Whitethroats in Morocco was 13.7 g, which accord-

ing to our data corresponds to a mean fat-score of between 0–2.

Conclusion

Blackcaps and Whitethroats which in spring (largely through feeding on *Maytenus* berries) put on fuel in The Gambia before the trans-Saharan passage may gain between 3 and 4% of their fat-free body mass per day. When ready for take-off about 35% of a Blackcap's and 40% of a Whitethroat's body mass consist of fuel for the trip. According to conventional flight-range calculations this gives them flight ranges in still air of around 1200 km, which will not take them unaided across the desert. But predictable tailwinds, usually found at altitudes above 2500 m, may help them to reach central Morocco or beyond. In addition, recent wind-tunnel experiments have suggested that a distinctly reduced drag coefficient should be used in the flight-range calculations. This may extend the still air range to more than 2500 km – allowing a desert crossing also without the help of tailwinds.

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Sammanfattning

Fettupplagring och möjliga flygsträckor hos svarthättor och törnsångare på vårflyttning i Gambia.

Inom ramen för ett sameuropeiskt forskarnätverk kring fågelflyttningen mellan Palaearktis och Afrika har brittiska och svenska ornitologer sedan 1995 bedrivit ringmärkning på Ginak Island i Gambia. Fångstmiljön är ett kustnära äldre dynlandskap, numera vuxet med acacior och diverse buskar och med tamarisksnår i fuktigare områden. Här förbereder sig många palaearktiska flyttfåglar för passagen över Sahara, vars södra gräns ligger blott 300 km norrut. Av största vikt för bränslepåfyllningen (fettupplagringen) inför ökenpassagen är bären på den vanligt förekommande busken *Maytenus senegalensis*.

Svarthättor och törnsångare som rastade på Ginak under uppladdningsperioden kring skiftet mars/april 1995 ökade sin kroppsmassa (vikt) med upp till 3–4 % per dag och när de var redo att ge sig iväg norrut (vid fettklasstatus 5–7 på en åttagradig skala som börjar med 0) bestod de till 35–40 % av bränsle – i huvudsak pålagrat fett. Enligt hittills använda normer för beräkning av fåglars potentiella flygsträcka skulle detta ge dem en räckvidd i vindstilla väder på ungefär 1200 km. Detta är emellertid inte tillräckligt för att ta dem över den 1500–2000 km breda öken,

där komplettering med föda och vatten sällan låter sig göras. Enda lösningen för fåglarna vore att utnyttja den medvind som normalt blåser på ca 2500 m höjd. Med hjälp av medvind skulle de med de observerade bränslereserverna kunna nå över öknen till acceptabla rastområden i Marocko. Dessa vindar är dock inte helt förutsägbara och medvind kan mer eller mindre utebli vissa år, något som då borde leda till populationskrascher av en storleksordning som sällan eller aldrig noterats.

Därför kunde man undra om beräkningarna verkligen var korrekta, och nu visar också vindtunnelförsök i Lund att den friktionskoefficient som använts i de tidigare beräkningarna troligen är kraftigt överskattad. Ett nytt, empiriskt och avsevärt mindre friktionsvärde ungefär fördubblar svarthättornas och törnsångarnas räckvidd i vindstilla väder, till mer än 2500 km. Detta räcker för att flyga över Sahara, även utan hjälp av medvind!

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

ÅKE LINDSTRÖM, ANDERS HEDENSTRÖM & JAN PETTERSSON

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. Juve-

nile 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-Saharan 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 & Haselquist 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 höstarna 1988, 1989 och 1990. Mediandatum presenteras endast för lokaler där minst 30 av respektive åldersgrupp fångats. Geografiska koordinater presenteras i Tabell 1.

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

Locality <i>Plats</i>	I/C	1988			1989			Ad
		Ad	Juv	Juv %	Ad	Juv	Juv %	
1 Ammarnäs	I	43	677	94	82	759	90	39
2 Haparanda S	C	29	1117	97	59	1823	97	215
3 Ännsjön	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 <i>Summa</i>		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

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.

1990			1988–1990		Total Summa
Juv	Juv %	Ad	Juv	Juv %	
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

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.

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

Locality <i>Plats</i>	1988		1989		1990	
	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 Åssön	–	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.

Locality <i>Plats</i>	Seasonal average <i>Medelvärde hösten</i>			Week 32 <i>Vecka 32</i>			Week 34 <i>Vecka 34</i>		
	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 Åssön	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.

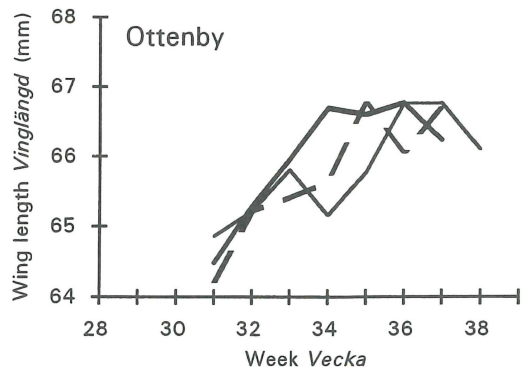
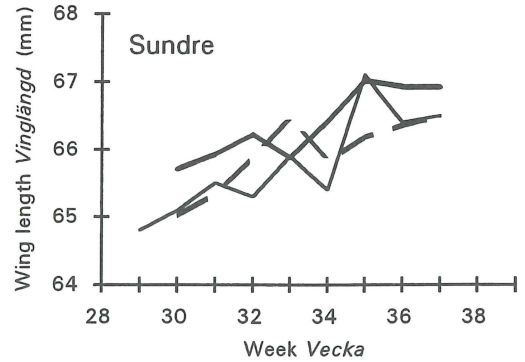


Fig. 2. Weekly average wing lengths (mm) of autumn migrating juvenile Willow Warblers at Ottenby (site 16) and Sundre (site 14). Data are shown for three years (1988: thick solid line, 1989: dashed line, 1990: thin solid line).

Medelvingslängd 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.

Locality Plats	1988		1989	
	Ad	Juv	Ad	Juv
1 Ammarnäs	0.85	1.03	–	1.19
2 Haparanda S	1.73	1.65	2.24	2.29
3 Ännsjön	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 kroppsuggning (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.

Locality Plats	1989				1990			
	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 Ännsjön	1.1	17 Aug	–	–	1.4	9 Aug	–	–
4 Eggegrund	–	–	–	–	–	–	3.0	16 Aug
6 Åssön	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

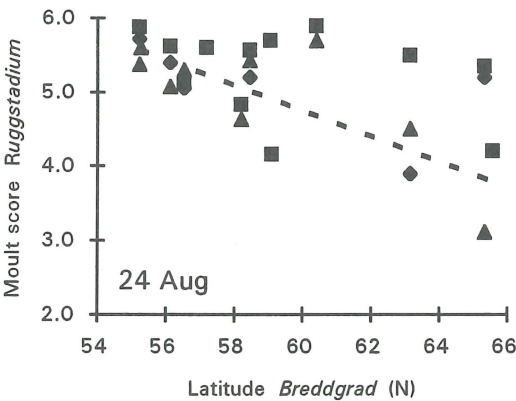
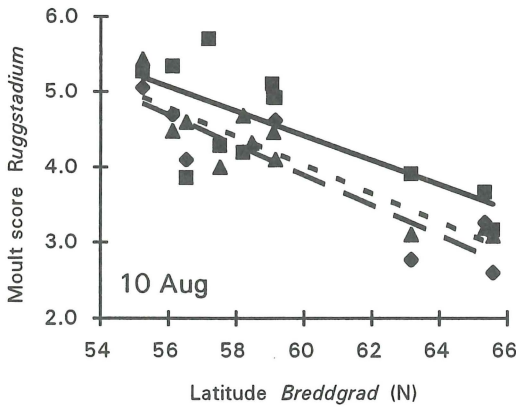


Fig. 3. Average juvenile moult scores in week 32 (approximately 10 August) and week 34 (approximately 24 August) in relation to latitude of ringing. Data are shown separately for the three study years (1988: ■, solid line; 1989: ◆, dashed line; 1990: ▲, dotted line). Lines are only presented for significant 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.

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 rela-

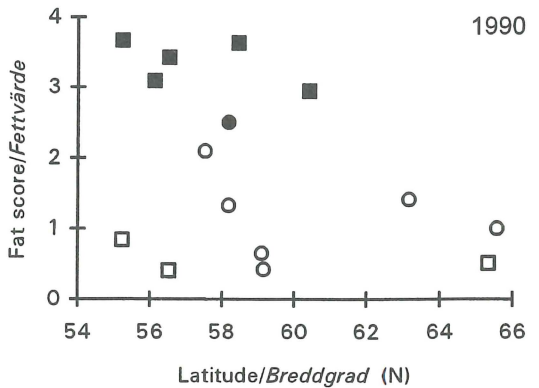
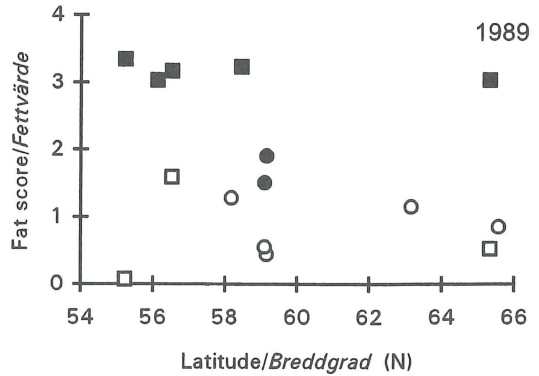


Fig. 4. Average fat scores of juvenile Willow Warblers in relation to latitude and locality type in the first week the average moult stage reached at least 3 and 5, respectively (□ = moult stage 3, coastal site; ○ = moult stage 3, inland site; ■ = moult stage 5, coastal site; ● = moult stage 5, inland 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.

tively 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

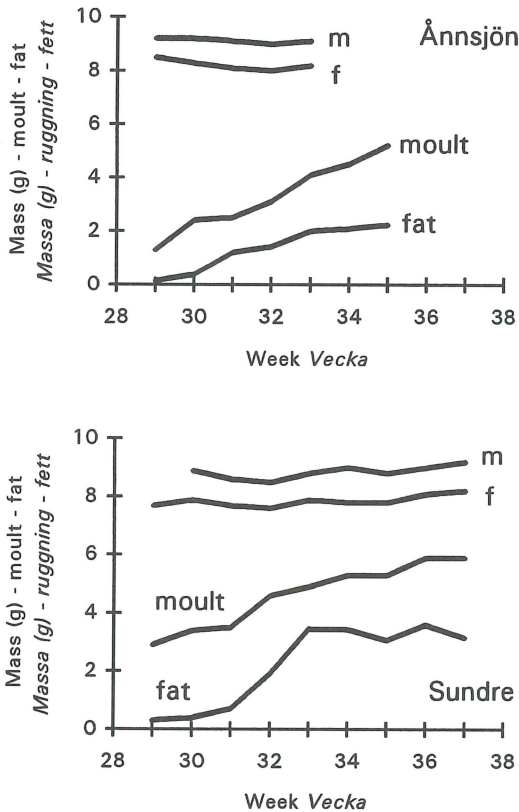


Fig. 5. Weekly averages of body mass (g, males and females treated separately), moult and fat score of juvenile Willow Warblers at a) Ånnsjön (site 3) and b) Sundre (site 14) in 1990. Values are only presented if at least 30 birds were caught each week.

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 ungfågglarna var minst 5. Samma tidsperiod är använd för adulta fåglar. De olika platsernas geografiska läge presenteras i Fig. 1.

Locality Plats	1989						1990					
	Ad			Juv			Ad			Juv		
	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.

Locality Plats	1989						1990					
	Ad			Juv			Ad			Juv		
	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.

Locality Plats	Males Hanar						Females Honor					
	1988		1989		1990		1988		1989		1990	
	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 kropps massa hos unga hanar och honor av lövsångare i olika stadier av kroppsuggning (MS). Värdena som presenteras är de genomsnittliga kropps massorna 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.

Locality <i>Plats</i>	Males <i>Hanar</i>						Females <i>Honor</i>					
	1988		1989		1990		1988		1989		1990	
	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 Ännsjön	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 popula-

tion 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 disproportionately 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 & Rhönnsstad 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.

Locality <i>Plats</i>	1988						1989			
	N_+	Ad N_k	%	N_+	Juv N_k	%	N_+	Ad 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 <i>Summa</i>	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

(Lawn 1984, Norman 1994).

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 (Pettersson 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.

Juv N _k	%	1990				Juv	
		N ₊	Ad 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

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

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 (Rog-

ers 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 & Rhönnsstad 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 & Rhönnsstad 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 disproportionately small fat stores (cf. Lindström & Alerstam 1986, Åkesson et al. 1996). Ehnbohm 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 night's flight (Baggott 1986). The average Swedish Willow Warbler would then have fat for about one night's flight. However, if birds arriving at coastal sites had already undertaken one night's 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 & Rhönningstad 1996). Also Finnish Sedge Warblers carry smaller fat loads than their British conspecifics (Koskimies & Sauola 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 re-trapped 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 (Bag-

gott 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 average 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 ring-

ers, 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	Ännsjön	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 <i>Fångstperiod</i>	CI	Catching period <i>Fångstperiod</i>	CI	Catching period <i>Fångstperiod</i>	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–24 Sep	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. ANCOVA, 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 aduler fångades för att tillåta en jämförelse av fettreserverna hos aduler 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 ungfågarna 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 övervintningskvarter 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 kroppsfjädruggning, 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. Könbestämning 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 hänvisning 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 kroppsfjädruggningen 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 ungfågglarna, medan det inte fanns någon skillnad mellan åldersklasserna i norra Sverige (Tabell 4). Hos ungfågglar 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 ungfågglar, 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 ungfågglar 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 ungfågglar 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 ungfågglar i fångsten var mycket hög både vid kust- och inlandslokaler (93%), vilket troligen inte representerar den verkliga proportionen ungfågglar i populationen på hösten (som borde vara 70–75%). Det är ett välkänt faktum att vid fågelstationer fångas normalt en högre andel ungfågglar än man borde förvänta sig. I samband med frontpassager eller oförutsedda väderomslag kan man dock ibland fånga en mycket lägre andel ungfågglar, som troligen bättre motsvarar den sanna andelen bland den överflygande populationen. Även vid inlandslokaler var andelen ungfågglar högre än man skulle ha förväntat sig, vilket troligen kan förklaras av att ungfågglar uppvisar spridningsrörelser innan den egentliga flyttningen och de är då lätta att fånga. Adulta fåglar däremot genomgår en komplett ruggning un-

der samma period och är då mycket orörliga och undgår därför att bli fångade i samma utsträckning som ungfågglarna. Det finns även den möjligheten att inlandslokaler 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 ungfågglarna och således inte rastar lika många gånger i Sverige.

Ungfågglarna passerade fångstplatserna i genomsnitt något före de adulta, en effekt som troligen uppstår på grund av den mer tidskrävande kompletta ruggningen hos adultar. Däremot fanns ingen tidskillnad i flyttningen mellan könen. Genom att använda ruggningsskalan för åldersbestämning av ungfågglar kunde vi visa att ungfågglar 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 ungfågglarna kommit längre i sin ruggning när de fångades på kustlokalerna, vilket förmodligen återspeglar att dessa fåglar verkligen gett sig iväg på flyttning. Fågglarna 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 ungfågglarna, 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 karakteriserar fåglarnas energidepåer och den följande diskussionen grundar sig på fettdata.

Vi fann indikationer på att adulta fåglar hade större fettreserver än ungfågglar i södra Sverige. Att adulta fåglar har större energireserver än ungfågglar under flyttningen är det mönster man normalt finner hos andra arter. Under första hälften av kroppsfjädderruggningen hade ungfågglarna 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

gen korta och inga stora energireserver krävs. Alternativt så tillåter fåglarnas energibudget inte någon kraftig fettackumulering samtidigt med den energi-krävande ruggningen och fåglarna kan inte öka sina fettreserver. Mot slutet av kroppsuggningen 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 tex 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.

Occupation and breeding parameters in the Great Tit *Parus major* and the Italian Sparrow *Passer italiae* in nest-boxes of different size

ALBERTO SORACE & CLAUDIO CARERE

Abstract

This study examined the preference for nest-boxes of two different dimensions (14x14x22 cm, hole diameter 3.7 cm, 'normal'; 25x25x35 cm, hole diameter 6 cm, 'large') for three breeding seasons in the Great Tit and the Italian Sparrow together with specific reproductive parameters. Sparrows showed a significant preference for normal boxes while tits seemed not to discriminate between large and normal boxes although in the large ones the breeding success was impaired by higher predation rates. For both species no differences between the two kinds of boxes

were found for date of laying. As regards clutch size, data suggest that in large boxes tits laid larger clutches.

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Introduction

In hole-nesting birds the selection of nest site is based on several characteristics such as risk of predation (Bellrose et al. 1964, Nilsson 1984, Blancher & Robertson 1985), degree of moisture in the cavity (Slagsvold & Lifjeld 1988), parasite infestation (e.g. Moss & Camin 1970, Møller 1989, Opplinger et al. 1994), presence of old nest material (Thompson & Neill 1991, Olsson & Allander 1995), and size of the cavity (e.g. Löhr 1973, van Balen 1984, Gustafsson & Nilsson 1985, Slagsvold 1989).

As regards the latter feature, most of the previous studies have analysed the relationship between the size of nest-boxes and clutch size in small hole-nesting passerines by using the bottom area as independent variable (e.g. Grakzyc 1967, Löhr 1973, Karlsson & Nilsson 1977, van Balen 1984, Gustafsson & Nilsson 1985). Data were collected in boxes with floors ranging from 25 cm² (Ludescher 1973) up to 314 cm² (Löhr 1973), boxes of 100–120 cm² being considered normal. Almost all the publications included the Great Tit among the species studied; this species was shown to have a preference for larger cavities (>150 cm², Löhr 1977, van Balen 1984, Gustafsson & Nilsson 1985), but differences

in dates of laying were observed only in one study (van Balen 1984). Clutch size was found to be adjusted to the available cavity space, the so-called "area effect", and this plasticity, whose mechanisms are unknown, was found at different degrees in many other species (e.g. Karlsson & Nilsson 1977, van Balen 1984, Gustafsson & Nilsson 1985). As regards breeding success, results are sometimes contradictory. For example, the risk of an hyperthermic state, which might result in increased mortality of the nestlings, has been demonstrated in broods reared in very small (36 cm²) boxes (van Balen 1984). Gustafsson & Nilsson (1985) also found a reduced breeding success in flycatchers (*Ficedula spp.*) nesting in smaller (57–87 cm²) boxes. However, in Great Tit Löhr (1973) found no differences between small (64 cm²) and large (314 cm²) boxes.

No data about box size preference are available neither for the Italian Sparrow, nor for the House Sparrow *Passer domesticus*, the latter being considered a more determinate layer in comparison with tits (Anderson 1989).

The present study was aimed at investigating the preference for two kinds of artificial nesting cavities with very different bottom area and entrance hole diameter in the Great Tit and the Italian Sparrow

Table 1. Occupation percentages of the two kinds of nest-boxes in Italian Sparrow and Great Tit in the three study areas.

Procent beläggning i de två holkyperna för italiensk sparv och talgoxe i de tre undersökningsområdena.

	Italian Sparrow <i>italiensk sparv</i>					Great tit <i>talgoxe</i>				
	normal <i>normala</i>	n	large <i>stora</i>	n	P	normal <i>normala</i>	n	large <i>stora</i>	n	P
Burano	55.6	54	6.7	15	0.01	28.4	74	44.4	18	0.30
Orbetello	24.7	77	9.5	21	0.25	10.3	97	16.7	24	0.90
Macchiagrande	55.6	54	64.3	14	0.80	51.4	114	31.2	18	0.20
All areas <i>Alla</i>	42.7	185	24.0	50	0.05	31.2	285	29.3	60	0.90

Data reported refer to three breeding seasons; n is the number of nest boxes available

Rapporterade data avser tre häckningssäsonger; n är antalet tillgängliga holkar

together with specific reproductive parameters (date of laying, clutch size, and breeding success).

The large boxes we used were very discernible and the hole entrance was very large (see below). Predictions were that i) both tits and sparrows prefer normal boxes because of higher predation risks in larger ones; ii) tits breeding in larger boxes lay larger clutches because of the area effect; iii) sparrows breeding in larger boxes do not increase clutch size because their potential to adjust it is low; iv) for both species breeding success is impaired in larger boxes.

Materials and methods

Field data were collected during three breeding seasons (1990–1992) in three woodland areas dominated by Mediterranean vegetation along the Thyrranian coast of Central Italy, namely Orbetello, Burano and Macchiagrande. Great Tits and Italian Sparrows are resident in these areas, and this gives the opportunity to inspect potential nest sites long before onset of breeding. In these study years sparrows started laying between 25 April and 5 May being often triple-brooded (pers. obs.) and tits between 1 April and 10 April being often double-brooded (Bellavita & Sorace 1994). Sparrows were usually breeding only in the outer parts of the woods. Potential competitors for nest sites were rats *Rattus rattus*, the Hoopoe *Upupa epops* and the Blue Tit *Parus caeruleus*, both bird species having very low population density (pers. obs.). Potential predators were the Four-line Snake *Elaphe quatorlineata*, the

Aesculapian Snake *Elaphe longissima*, the Western Whip Snake *Coluber viridiflavus*, rats (*Rattus sp.*) and the Weasel *Mustela nivalis*.

In January 1990, 62 'normal' (14x14x22 cm, hole diameter 3.7 cm, bottom area 196 cm²) and 20 'large' (25x25x35 cm, hole diameter 6 cm, bottom area 625 cm²) nest-boxes were attached to trees 3 m above the ground and spaced 50 m. The large boxes were regularly scattered among the normal ones.

For sparrows, only boxes in the outer parts of the wood were considered available. In case of tits, which are known to prefer a clean cavity (Perrins 1979), after the first brood fledged, boxes with rests of a successful nest were considered not available for other females.

From 1 April up to 7 July in Burano and Macchiagrande nest-boxes were checked weekly, in Orbetello they were checked every 15 days. The parameters considered were percentages of occupation, date of laying, clutch size, predation rate, and breeding success. Nest-boxes were considered occupied when at least one egg was found inside. Dates of laying were recorded assuming that in both species the female lays one egg per day (Kluijver 1951, Lack 1955, Summers-Smith 1963). Because of the influence of the date of laying on clutch size (Kluijver 1951, Lack 1955), comparisons between large and normal boxes were performed considering only clutches laid during corresponding periods in the three years. Predation rate was the percentage of clutches and/or broods that failed because of predation. For each brood breeding success was calculated

Table 2. Date of laying (mean), clutch size (mean) and breeding success (mean %) in Italian Sparrow and Great Tit for the two kinds of nest-boxes.

Läggingsdatum (medel), kullstorlek (medel) och häckningsframgång (medel %) för italiensk sparv och talgoxe i de två holkyperna.

	Italian Sparrow <i>italiensk sparv</i>							Great tit <i>talgoxe</i>						
	normal <i>normala</i>	n	s.e.	large <i>stora</i>	n	s.e.	P	normal <i>normala</i>	n	s.e.	large <i>stora</i>	n	s.e.	P
Date of laying <i>Läggingsdatum</i>	45.0	61	0.9	45.3	9	2.2	0.90	13.4	39	1.6	14.0	14	2.5	0.85
Clutch size <i>Kullstorlek</i>	5.1	21	0.2	5.5	11	0.3	0.20	7.0	17	0.4	7.9	14	0.5	0.20
Breeding success <i>Häckningsframgång</i>	57.7	63	5.4	45.9	10	13	0.45	67.5	81	4.3	36.1	17	10.3	0.01

Data reported refer to three breeding seasons and three study areas

Rapporterade data avser tre häckningssäsonger och tre områden

s.e. = standard error

Day 1 = 1 April *Dag 1 = 1 april*

ed as number of nestlings/number of laid eggs x 100. At Orbetello, because of larger intervals between inspections, it was not possible to evaluate breeding success in 42% of the broods.

Data on percent of occupation and predation rate were analysed by χ^2 test. Data on reproductive parameters were analysed by Student t-test; because of the non-normal distribution, data on breeding success were arcsin transformed and data on clutch size square root transformed prior to the parametric analysis (Fowler & Cohen 1984).

Results

Overall sparrows showed a significant preference for normal boxes. However, in Macchiagrande there were small differences in the occupation of the two kind of boxes (Table 1). Tits did not discriminate between large and normal boxes (Table 1).

No significant differences for date of laying were observed in any of the species (Table 2). As regards clutch size, tits laid on average more eggs in large boxes; however, this trend did not reach statistical significance (Table 2). Breeding success in large boxes was significantly lower than in normal ones for tits but not for sparrows (Table 2). This was, as expected, due to a higher predation rate, at least in tits (33.3% vs. 6%; $\chi^2_1 = 7.99$, $p < 0.01$). For sparrows total predation rate was higher in large boxes (30% vs. 17%), although data collected were too scarce to allow statistical analysis. In tits predation rate for both kinds of boxes was higher in Burano when

compared with all others areas (24.1% vs. 6.2%; $\chi^2_1 = 4.0$; $p < 0.05$).

Discussion

Our results show that only sparrows discriminated between the two kinds of nest-boxes and preferred the normal ones. In this species, the potential to increase the clutch size is low (Anderson 1977, Murphy 1978, Pinowska 1979, Anderson 1989), and the opportunity to lay a higher number of eggs in larger cavities is reduced. Among the species studied only in the Starling *Sturnus vulgaris* the size of the bottom area had no effect on clutch size (e.g. Moed & Dawson 1979, Karlsson & Nilsson 1977). Interspecific differences have been attributed to the size of the species, that could affect the amount of energy lost from the brood filling the nest cavity (Karlsson & Nilsson 1977); in our study the response of the heavier species (Italian Sparrow) to an unusually large nest site seemed to be weaker.

On the other hand tits, for which the potential to increase clutch size is higher, showed no discrimination in spite of an impaired breeding success in large boxes. However, in this species the possibility to lay a larger clutch is limited, since in the Mediterranean area clutch size is generally lower than in other European populations (Blondel et al. 1987, Isenmann 1987, Bellavita & Sorace 1994). It is likely that this feature could have partially buffered the area effect. Differences between areas are more difficult to interpret; however, we note that in Burano

where the highest predation rates were recorded, tits showed preference for the normal boxes. It must be pointed out that other factors such as age, intraspecific competition, and nesting site availability can play important roles in the choice of the nesting cavity (Nilsson 1984, Barba & Gil Delgado 1990, Cramp & Perrins 1993), and can affect the individual choice of nest site.

As regards the temperature to which the offspring can be exposed van Balen (1984) reported that a large brood (>8 young) of Great Tit in a small cavity (36 cm²) could run the risk of hyperthermia over a threshold value of 20 °C. This temperature is easily reached and exceeded in the Mediterranean area and this element should be considered with more attention as a selective factor for nest size choice. However, at least in tits, females nesting in large cavities may completely cover the bottom with moss and other isolating materials thus assuring a good thermic stability.

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Sammanfattning

Beläggning och häckningsparametrar för talgoxe Parus major och italiensk sparv Passer italiae i holkar av olika storlek

Bland hålhäckande fåglar påverkas valet av boplatser av flera faktorer såsom predationsrisk, fuktighet i bohålan, parasitförekomst, gammalt bomaterial och hållighetens storlek. Flera studier, de flesta på småfåglar, särskilt talgoxe, har gjorts av holkar med bottenyta från 25 till 314 cm². Hos flera arter har man påvisat att holkstorleken har effekt på kullstorleken och för talgoxe att den föredrar holkar som har en bottenyta större än 150 cm². Uppgifter om holkstorlekens inverkan på kullstorleken saknas för såväl gråsparv som italiensk sparv.

Denna studie syftar till att studera holkvalet för talgoxe och italiensk sparv för holkar med mycket olika bottenyta och håldiameter samt att studera datum för äggläggning, kullstorlek och häckningsframgång i de olika holkarna. Undersökningen utfördes 1990–1992 i tre områden med medelhavsvegetation i centrala Italien. Både talgoxe och italiensk sparv är stannfåglar året om i dessa områden, där talgoxen ofta lägger två och sparven tre kullar.

De två holktyper som användes var ”normala” (bottenyta 196 cm², håldiameter 3,7 cm; 62 stycken) respektive ”stora” (bottenyta 625 cm², håldiameter 6

cm; 20 stycken). De sattes upp i januari 1990, 3 m högt och 50 m från varandra, med de stora holkarna jämt spridda bland de normala. Holkarna kontrollerades veckovis i två och var femtonde dag i ett av områdena mellan 1 april och 7 juli.

Vi fann att sparvarna föredrog normala holkar framför stora i två av områdena, medan inga skillnader noterades för talgoxe. Det fanns ingen skillnad i läggningsdatum mellan normala och stora holkar för någon av arterna. Det fanns en tendens till större kullar i de större holkarna, men skillnaderna var inte signifikanta. Häckningsframgången var däremot lägre i de större holkarna för talgoxe medan det bara var en obetydlig skillnad för italiensk sparv. Skillnaden berodde på högre predation i de större holkarna. För talgoxe var predationen 33% i de stora mot 7% i de små holkarna, medan skillnaden var mindre 30% mot 17% för sparvarna, och den senare skillnaden var inte signifikant.

Att vi inte fick något svar på kullstorleken med ökad holkstorlek för italiensk sparv var väntat eftersom det är känt att arten liksom den närbesläktade gråsparven har ringa förmåga att modifiera antalet lagda ägg. För talgoxe hade vi däremot väntat en effekt av holkstorleken. Att denna uteblev kan bero på att talgoxen i Medelhavsområdet har mindre kullstorlek än i andra europeiska populationer, vilket kan ha buffrat yteffekten.

Short communications *Korta rapporter*

Elva ägg i en holk med stare *Sturnus vulgaris* – tre honor lade i samma holk?

SÖREN SVENSSON & SVEN HELLQVIST

Hos staren förekommer det förhållandevis ofta att mer än en hona lägger ägg i samma holk. Oftast är det fråga om att en hona varit inne och lagt något enstaka ägg bland äggen i en annan honas kull. Äggen har sedan ruvats fram av den "ordinarie" honan. Den normala kullstorleken för stare är 4–6 ägg med 5 ägg som det allra vanligaste. När äggantalet överstiger sex ägg har man i regel anledning att misstänka att ett eller flera av äggen är s.k. parasitägg.

Sedan 1980 har ett stort antal starholkar kontrollerats inom ramen för det miljöövervakningsprogram som naturvårdsverket driver, med den ene av författarna (SS) som projektledare. Under samtliga år har det registrerats 6.518 kullar där minst ett ägg lagts. Av dessa har 5.693 stycken registrerats som "full kull", d.v.s. att läggningen upphört och ruvning påbörjats. För de övriga 825 kullarna har ruvningen med säkerhet avbrutits före full kull eller det har inte varit möjligt att säkert bestämma om full kull lagts. Antalet kullar med olika antal ägg framgår av Tabell 1. Fram till och med 1995 var det maximala antalet ägg nio (två fall). Men 1996 registrerades rekordet 11 ägg i en holk i Umeå under de holkkontroller som den andre av författarna (SH) svarar för sedan flera år tillbaka i detta område.

I denna holk med elva ägg hade stararna byggt en bale den 8 maj, utan att ännu ha lagt några ägg. Fyra dagar senare, den 12 maj, fanns 6 ägg. Eftersom staren bara lägger ett ägg om dagen måste två honor ha deltagit i äggläggningen nästan från början. Den 19 maj fanns 8 ägg. Här borde äggläggningen ha varit avslutad, men vid nästa kontroll den 27 maj fanns 11 ägg! Samma antal ägg fanns kvar vid en

senare kontroll den 7 juni. Vid samtliga tillfällen var äggen kalla, och ingen hona observerades i holken vid något tillfälle. De elva äggen blev således sannolikt aldrig ruvade och resulterade heller aldrig i några ungar. Det är osannolikt att någon av de honor som lade de första äggen skulle ha återupptagit läggningen efter den 19 maj och lagt ytterligare 3 ägg. Det måste rimligtvis ha varit en tredje hona, eller kanske till och med mer än en hona som lagt dessa tre extra ägg.

Holken med elva ägg ingick i en grupp om fem holkar. En holk var sprucken, och i sprickan fastnade och dog en starhona. Trots detta låg ett ägg på holkens botten (utan bale) vid nästa besök, men mer än så blev det inte. I två av holkarna byggdes bale, men häckningarna övergavs innan några ägg lagts. I den fjärde holken lades det första av sex ägg den 9 maj, d.v.s. samtidigt som första ägget i holken med elva ägg bör ha lagts, och denna kull resulterade i fem ungar.

De två ovannämnda fallen med nio ägg härrör från Revinge i Skåne 1981 och Ottenby på Öland 1991. I Revingefallet fanns 3 ägg den 7 maj (läggningen hade således började den 5 maj). Den 9 maj, två dagar senare, fanns 5 ägg, så långt alltså normal läggningstakt med ett ägg om dagen för en hona. Men två dagar senare, den 11 maj, fanns 8 ägg och den 14 maj 9 ägg. En ytterligare hona hade således lagt tre extra ägg den 10–12 maj. Denna honas första ägg lades således fem dagar senare än den första honans första ägg. Åtta av ungarna kläcktes, men två av dem försvann snabbt och ett ägg med embryo förblev oklänkt. Sex ungar blev flygga. Med all sannolikhet var det den första honans sex ägg som blev framgångsrika. Nioäggshäckningen vid Ottenby startade den 28 april och 2 ägg hade lagts den 29 april. Den 3 maj fanns 7 ägg och den 6 maj 9 ägg. Även här hade således en extra hona lagt tre ägg med start fem dagar efter den första honan. I detta fall kläcktes alla nio äggen. En av ungarna dog redan efter några få dagar och ytterligare två ungar efter

Tabell 1. Kullstorleken för stare registrerad inom naturvårdsverkets bevakningsområden i Sverige.

Clutch size of the Starling recorded within the monitoring areas of the nature conservation agency in Sweden.

Antal ägg <i>No. of eggs</i>	Fulla kullar <i>Full clutches</i>	Övriga <i>Remaining</i>
1	4	367
2	28	256
3	143	146
4	1026	52
5	2734	3
6	1494	1
7	232	0
8	29	0
9	2	0
10	0	0
11	1	0
>11	0	0
Summa <i>Total</i>	5693	825

någon vecka. Slutresultatet blev sex flygga ungar, sannolikt även här den första honans kull. Orsaken till förlusterna var säkert i båda fallen den andra honans fem dagar senare läggning, vilket resulterade att hennes ungar inte klarade konkurrensen med de först kläckta och därför större ungar från den första honans ägg. Parasitläggning kan därför antas ha ganska ringa framgång såvida inte parasithonan lyckas prångla in sina ägg tidigt under förstahonans läggning och inte som i dessa två fall med början när första honan lade sitt sista ägg.

I fallet med elva ägg i Umeå lades 6 ägg under loppet av fyra dagar. Det innebär att andra honan började senast två dagar efter första honan. Det är till och med möjligt att de började samtidigt. Det är möjligt, eller kanske till och med sannolikt, att det i detta fall inte var fråga om parasitism i sedvanlig bemärkelse utan om två honor som aktivt konkurrerade om samma holk, båda i avsikt att ruva äggen. Beskrivningen ovan av situationen i den grupp om fem holkar där holken med elva ägg ingick tyder på att det rådde konkurrens om just dessa holkar. I övriga 95 holkar som fanns i kontrollområdet var det nämligen bara påbörjad häckning (bale) i fem och full kull lagd i sex holkar. Den sedvanliga parasitismen är inte aggressiv utan den parasiterande honan lägger sina ägg när den första honans bevakning fallerar; den senare vet således i regel inte om att hon fått fler ägg än hon lagt att ruva. Det kan således vara

den aktiva, och kanske högst aggressiva konkurrensen om holken och äggen som resulterade i att det aldrig blev någon ruvning av. Den tredje honan, som kom in i bilden med tre ytterligare ägg bra mycket senare, kan ha varit en ordinär parasithona, som lade sina ägg utan att ha avsikt att ruva dem, vilket är normalt för en sådan hona. Hon gjorde dock i så fall misstaget att lägga sina ägg i en redan övergiven kull.

Det förekommer ytterst sällsynt att två honor lägger ägg i samma holk och gemensamt och i sämja föder upp ungar. Ett fall har rapporterats från Nordamerika av Stouffer m. fl. (1988) och ett andra fall från Belgien av Vanvinckenroge (1968). I det senare fallet var det dock två honor i en stor uggleholk som hade var sitt bo bredvid varandra. I det förstnämnda fallet var det två honor och en hane som var involverade. Ett tredje fall, i Belgien, är särskilt intressant eftersom man med DNA-analys bestämde ungararnas föräldraskap (Pinxten m.fl. 1994). Även här var det två honor och en hane som svarade för häckningen. Holken innehöll tio ägg. Fem av äggen var mörkare och mindre än de övriga fem, men respektive femportion var inbördes lika. Eftersom olika honor ofta lägger ägg med olika färg, form och storlek, men var och en har mycket lika ägg, fanns redan tidigt misstanke om att det rörde sig om just två honor. När sedan DNA-analyserna utförts med hjälp av blodprover från de tre föräldrarna och nio av ungarerna (ett ägg var obefruktat) visade det sig att ena honan var mor till fem av ungarerna, den andra till fyra av ungarerna och hanen far till samtliga nio ungar. Det rörde sig således om ett äkta fall av "kommunal" häckning. Alla tre föräldrarna deltog i matningen av ungarerna, men eftersom man inte hade haft holken under kontroll under ruvningsperioden vet man inte om båda honorna ruvade. Författarna tror dock att så måste ha varit fallet eftersom andra data tyder på att tio ägg inte kan ruvas av en ensam hona.

Kommunala häckningssystem finns i hög frekvens hos flera arter, bl.a. hos en del afrikanska starar, men som sagt ytterst sällan hos vår stare. Men enstaka fall av kommunal häckning har rapporterats från åtskilliga arter som normalt är socialt monogama. En av författarna har exempelvis varit med om att följa ett bo av ängspioplärka där två honor tillsammans, sida vid sida, ruvade 11 ägg i en trång håla (Fredriksson & Svensson 1984). Det faktum att kommunal häckning är sällsynt hos stare innebär däremot inte att det oftast råder genetisk monogami i starkullarna. Förutom förekomsten av parasitägg från olika honor, som kan finnas i upp till 40% av bona (Pinxten m.fl. 1991), förekommer frekventa

parningar utanför det sociala paret, omfattande upp till ca 30% av kullarna och ca 10% av ungarna (Smith & Schantz 1993, Pinxten m.fl. 1993). Andra avvikelser från det monogama systemet är hög frekvens av polygyni: i upp till 37% av häckningarna hade två honor samme hane (Pinxten m.fl. 1989).

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Summary

Eleven eggs in a Starling Sturnus vulgaris nest box – three females laying in the same box?

The most common clutch size of the Starling is five eggs with four or six eggs also being common. Among 5693 complete clutches, recorded in a monitoring scheme operated by the nature conservation agency, there were only two cases with more than eight eggs (Table 1). In 1996 one nest box with 11 eggs was found near Umeå in northern Sweden. The box contained a nest without eggs on 8 May. Four days later, on 12 May, the nest contained 6 eggs. Since the Starling lays only one egg a day, two females must have laid simultaneously. On 19 May, 8 eggs had been laid, but on 7 June there were 11

eggs! The eggs were cold on all visits, and no adult bird was ever observed in the nest box. Hence, the eggs were probably never incubated and they never hatched. It is unlikely that any of the first two females later returned to resume egg-laying after 19 May. A third female must have laid the three extra eggs, or possibly more than one new female.

It is fairly common that females dump eggs in the nest of other females, so called brood parasitism. Such parasitism usually involves only one or two eggs. It is very unusual that two female Starlings lay eggs simultaneously from the start in the same nest. In the two cases with nine eggs mentioned above, three of the eggs had been laid later than the eggs of the first female. In both cases the first of the three extra eggs had been laid on the day when the first female laid her fifth egg. In both cases only the eggs of the first female resulted in fledged young, the other young died during the very first days after hatching, probably because they were too small to compete with the other young.

Successful breedings of two females in the same nest box have been reported a few times. Stouffer et al. (1988) reported such a case from North America (one male and two females). Another one was reported from Belgium by Vanvinkenroge (1968), but in that case the two females had separate nests in a large owl nest box. A third case, also from Belgium (Pinxten et al. 1994), is particularly interesting. The nest box contained ten eggs, of which nine hatched. One male and two females cared for the young. DNA fingerprinting of blood samples from the three adults and the nine young showed that the male was father of all young, and the two females were mothers of five and four young. Thus, this was a case of true communal breeding.

Since in our case, two females continued to lay eggs simultaneously from the start or almost from the start, eight eggs in total, they may have done so in harmony. But since they both deserted the clutch, it is perhaps more likely that they competed aggressively so that they were not able to maintain efficient incubation.

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Nya böcker *New books*

R. Wehner, M. Leherer & W. R. Harvey (red.) 1996. **Navigation.** *Journal of Experimental Biology*, Vol. 199 (1), 261 pp. ISBN 0 948 601-52-3. (£29, The Company of Biologists Ltd., Bidder Building, 140 Cowley Road, Cambridge CB4 4DL, UK)

Föreliggande skrift är en specialutgåva av den vetenskapliga tidsskriften *Journal of Experimental Biology* (JEB), och utgör det samlade resultatet av en konferens om navigation hos djur som nyligen hölls i Cambridge, augusti 1995. Hela 33 översiktsartiklar behandlar principer och mekanismer som är involverade från storskalig navigering (bl.a. fåglars flyttning), navigering i mellanskan (framför allt hur insekter navigerar i sin omgivning) till småskalig navigering (hur främst insekter minns och hittar den sista biten till boet eller en födokälla). Även om detta temanummer av JEB behandlar navigation principiellt, så finns mycket matnyttigt att inhämta för den mer strikt ornitologiskt intresserade. Framförallt avsnittet om storskalig navigering innehåller många artiklar som berör fåglar.

Totalt är 12 artiklar enbart eller delvis om fåglar. Ken och Mary Able sammanfattar sin mångåriga forskning om orienteringssinnets utveckling hos en nordamerikansk tätting. De försöker utreda hur olika kompasser (magnetfält, stjärnor, solen, polariserat ljus) är relaterade till varandra och hur de används under flyttningen. Thomas Alerstam visar hur man med hjälp av olika metoder kan kartlägga fåglars flyttningssvägar och rörelser i olika skalor och hur dessa sedan kan användas för att besvara frågor om vilka kompasser de använder på sina flyttningsresor. Till skillnad från många andra forskare, som mestadels studerar hur fåglar betar sig i labmiljö, så får vi genom Alerstams metoder snarare svar på frågan hur fåglarna verkligen gör i naturen, något som ibland kanske glöms bort av ivriga labbaserade forskare. Paret Wolfgang och Roswitha Wiltschko samman-

fattar sina egna studier om magnetkompassen hos fåglar, som nu påvisats hos 18 olika arter. Det återstår emellertid att utreda vilken betydelse den har för fåglarna under deras flyttning.

Charles Walcott behandlar hur brevduvor hittar hem. Det framgår att även duvor kan använda olika typer av information för att hitta rätt. Det verkar även som om duvor uppfödda på olika platser föredrar olika system för sin navigering. En hypotes går ut på att brevduvor kan använda sig av en doftkarta i landskapet för sin orientering. Sedan denna hypotes först framkastades av italienska forskare i början på 70-talet har debatten om hur doftresultaten skall tolkas gått hög. På konferensen hade man därför arrangerat en "duell" mellan en av advokaterna (Hans Wallraff) och en av kritikerna (Roswitha Wiltschko) till dofthypotesen. Jag kan intyga att debattduellen höll vad den lovade och att röster höjdes i falssett. I tre artiklar kan man nu ta del av argumenten för och emot och själv bilda sig en uppfattning i frågan om huruvida duvor luktar sig fram genom landskapet eller ej.

Eberhard Gwinner skriver om hur fåglars flyttning kontrolleras av programmerade dygns- och årsrytmer. Andreas Helbig behandlar den genetiska komponenten som styr fåglars val av flyttningsriktning. Marcel Klaassen behandlar energetiska begränsningar för fåglars flygkapacitet. F. Papi och P. Luschi redovisar resultat från satellitföljningar av radiosändarförsädda havssköldpaddor och albatrosser.

I avsnittet om navigering i mellanskan finns en artikel om fåglar. David Sherry och Sarah Duff redogör för en serie experiment som syftar till att förklara hur fåglar kan hitta tillbaka till sin hamstringsgömma.

Förutom de artiklar med en stark ornitologisk koppling tycker jag att även Lincoln Browsers fascinerande redogörelse för monarkfjärilens flyttning förtjänar att nämnas. Detta temanummer av JEB

utgör den färskaste uppdateringen av navigationsforskningen. För forskare inom fältet är den givetvis ett självklart köp, men även till mer allmänt flyttningssintresserade amatörer kan jag starkt rekommendera den.

ANDERS HEDENSTRÖM

Dansk Ornitologisk Forenings Fugleregistreringsgrupp, 1996: **Vinterfugletælling 1995/96**. 20 sid. Dansk Ornitologisk Forening, Köpenhamn.

Dansk Ornitologisk Forening startade sin vinterfågelräkning samtidigt som vi gjorde det i Sverige, nämligen vintern 1975/76. Metoden är densamma som vår, rutter med 20 punkträkningar om 5 minuter vardera. Till skillnad från i Sverige räknar man bara en gång varje år, nämligen under perioden 20 december till 20 januari. Från färre än hundra rutter de första åren har antalet ökat till över två hundra de senaste åren. Rutterna fördelar sig ungefär lika mellan öarna och Jylland.

Mycket av det vi sett från den svenska vinterfågelräkningen återkommer i den danska. Skrattnåsen minskar i Danmark liksom i Sverige, både sommar- och vintertid. Minskningen som övervintrare har varit mycket drastisk i Danmark sedan 1990. Större hackspett och svartmes varierar i takt med granens frösättning och andra fröätare i takt med exempelvis bokens ollonskörd. Gårdsmygen har haft en serie år med höga tätheter under de åtta milda vintrarna 1987–1994. Skatan har visat en långsiktig ökning men stabiliserat sig under senare år.

Rapporten är en sedvanlig årsrapport utan djupare analyser. Det viktigaste är tabellen med de årliga indexvärdena som öppnar för analyser, såväl inom Danmark som i jämförelse med andra länder. Liksom allt miljöövervakningsarbete kräver dessa vinterräkningar mångårig uthållighet. På samma sätt som meteorologiska data kan fågelräkningar ge underlag för verkliga analyser först efter flera decennier. Det är därför med viss oro jag noterar att antalet rutter minskat något under de senaste fyra vintrarna. Danmark är dock ett relativt litet land, varför 200 rutter ändå ger ett bra underlag för att följa utvecklingen för ett stort antal arter.

SÖREN SVENSSON

Greifvögel und Eulen, Wangenheimstr. 32, D-14193 Berlin, Tyskland. 549 sid. Berlin. ISBN 3-9801961-1-9.

The World Working Group on Birds of Prey and Owls (WWGBP) drivs från tre platser, Berlin, London och Paris. Adressen till den tyska finns ovan och adressen till den engelska är c/o Robert D. Chancellor, 15b Bolton Gardens, London SW5 0AL, England. På omslagets andra sida finns information om gruppen: Den har funnits i mer än tjugofem år, omfattar över ett tusen rovfågelspecialister över hela världen och välkomnar alla rovfågelsentusiasiter som medlemmar. Man ger ut ett nyhetsblad två gånger om året. En av gruppens huvuduppgifter är att arrangera en världskonferens vart femte år. Nästa konferens (den femte) kommer att hållas i Johannesburg den 4–11 augusti 1998.

Denna bok innehåller ett stort antal uppsatser om örnar, hela sextiofyra stycken. Det rör sig om föredrag från tre olika möten, det första i Polen om havsörn och mindre skrikörn 1991, det andra (gruppens fjärde världskonferens) i Berlin 1992 och det tredje i Ungern om kejsarörn 1993. Majoriteten av uppsatserna är statusrapporter om arternas förekomst i olika länder och områden, analyser av hotbilder och beskrivningar av skydds- och restaureringsplaner samt sammanställningar av den mera långsiktiga utvecklingen av populationerna och deras reproduktionsresultat. Boken har alltså ett mycket stort värde för arbetet med att skydda rovfågelbestånden, vilket demonstreras av att boken publicerats med ekonomiskt stöd av WWF Tyskland och European Haliaeetus Association. Även om flertalet uppsatser är regionalt deskriptiva finns också flera med djupare analyser.

I en uppsats redovisas en studie av mitokondriskt cytokrom b hos fem *Aquila*-arter, särskilt inriktad på att bestämma om den spanska kejsarörnen är en egen art. Det visade sig att den spanska kejsarörnen *adalbertii* skilde sig lika mycket från nominaten *heliaca* som de två odiskutabla arterna större och mindre skrikörn skilde sig från varandra. Man drar slutsatsen att den spanska kejsarörnen är en egen art som inte haft någon genflöde från nominaten på mycket lång tid.

I en uppsats redovisas mindre skrikörnens flyttning. Ringåterfynden är tillräckligt många för att övervintringsområdet klart kan fastställas till östra delen av södra Afrika söder om ekvatorn. Merparten av sträcket går som bekant öster om Medelhavet. Det gäller sannolikt i varje fall adulta fåglar. Återfynden under första hösten är däremot vida spridda

B.-U. Meyburg & R. D. Chancellor (redaktörer), 1996: **Eagle Studies**. Weltarbeitsgruppe für

och antyder att passagen kanske sker på åtskilliga ställen, inte minst från södra Grekland via Kreta. Man har också använt nummerade vingmärken, vilket tycks fungera i viss utsträckning för att följa fåglar i närområdet efter häckningen och för att identifiera återvändande individer. Den kraftfullaste metoden är eljest de nya satellitföljningarna av radiosändarförsedda fåglar. En örn kunde följas från Mecklenburg, där den som unge försågs med sändare den 30 juli. Den stannade på häckningsplatsen till 11 september och gav sig sedan av mot sydost. Den förflyttade sig i jämn takt och passerade Bosporen den 28 september, nådde Turkiets sydkust den 3 oktober men sköts sedan i Libanon fyra dagar senare. Samma öde drabbade ett par andra ungfåglar, medan några av de adulta klarade sig till övervintringsområdet. Skrikörnar har också försett med sändare i övervintringsområdet och kunnat följas till Europa. Dessa intressanta studier finns redovisade mera i detalj i en annan uppsats, där också metodiken går igenom i detalj. Bl.a. visas en karta för en av de örnar som kunnat följas hela vägen från häckningsplatsen till övervintringsområdet i Zambia och tillbaka till tyska Östersjökusten.

I en uppsats redovisas anmärkningsvärda ansamlingar av minde skrikörnar i Brandenburg, där man under juni noterat upp till fyrtio fåglar inom små områden. Det måste röra sig om ännu ej köns mogna fåglar, många säkerligen inte av lokalt ursprung. Det är väl känt att skrikörna kan uppehålla sig långa tider på platser där de inte häckar. Ett par av de nyssnämnda sändarförsedda fåglarna uppehöll sig när de återkom till Europa i suboptimala biotoper i områden där häckning inte förekommer.

Nordiska örnforskare lyser i stort sett med sin frånvaro i boken. Jag hittar bara en uppsats, en studie av en kungsörnpopulation i Møre och Romsdal i Norge. Häckningsutfallet var i genomsnitt typiskt för skandinaviska förhållanden, 1,3 ungar per häckande par och 0,6 ungar per besatt revir. Anmärkningsvärt var att häckningsframgången sjunkit kraftigt efter 1982 med två år, 1987 och 1990, utan några flygga ungar alls i de arton undersökt bona. Det fanns en korrelation mellan häckningsframgången och förekomsten av hare, men några närmare tolkningar gör inte författaren.

Boken innehåller en oerhörd mängd fakta om örnar, av särskilt stort värde för alla som arbetar med att bevara deras bestånd. Även den som är allmänt intresserad av rovfågelnas biologi hittar mycket matnyttigt. Boken försvarar alltså mer än väl sin plats på bokhyllan, i synnerhet som faktakälla, även om den mera vetenskapligt inriktade forskaren fin-

ner många av uppsatserna ytliga. Men så blir det i allmänhet när man samlar föredrag från konferenser i en bok.

SÖREN SVENSSON

Stellan Hedgren, Tuomo Kolehmainen & Lars Tydén, 1996: **Inventering av häckande fåglar på gotländska strandängar 1996**. Länsstyrelsen i Gotlands län, Livsmiljöenheten, Rapport nr 6. 251 sid. Visby.

Av naturvårdsverkets rapport *Ängs- och hagmarker i Sverige – resultat av den landsomfattande inventeringen* (publicerad 1995, utförd 1987–1992) framgår att det finns 8.500 ha havsstrandäng. Så mycket som en femtedel av denna areal finns på Gotland, som därmed har ett alldeles särskilt ansvar för denna fågelrika biotop. Gotlands länsstyrelse gjorde därför en fågelinventering av sin strandängar våren 1996, och föredömligt snabbt föreligger nu en utförlig rapport. Den består av 12 sidor koncis sammanfattning och sedan detaljer om vart och ett av totalt 119 strandängsområden med en sammanlagd areal av 2.452 ha.

Sammanlagt registrerade man drygt 8000 fågelpar av 32 arter tillhörande grupperna svanar, gäss, simänder, vadare, måsfåglar, tärnor och gulärta. Övriga arter inventerades ej. Områdena varierade mycket i artrikedom, men de flesta områden hade mellan tio och tjugo arter. Även tätheten varierade kraftigt, från bara 0,2 par per ha inom ett 10 ha stort svagt till ej alls hävdad område vid Närshamn ("Överraskande fågeltomt" står det i kommentaren) till 25 par per ha i ett 8 ha stort, måttligt till svagt hävdad område inom Hamra socken (fast där ingick en nyetablerad skrattnåskoloni med 99 par, som dessutom kanske fungerat som magnet på flera av de övriga 17 arterna).

Den talrikaste arten totalt var tofsvipan med 948 par, varefter följde strandskata (724) och rödbena (721 par). Fåtaligast var ljunpipare (3) och dvärgmåås (1 par i en skrattnåskoloni på Faludden). En anmärkningsvärd siffra är 23 par stjärtand, en alarmerande minskning från 150 par vid en inventering 1981. I stort tycks dock de flesta arter ha klarat sig bra även om det delvis är svårt att göra säkra jämförelse på grund av bristande information från förr. Själv blev jag överraskad över att det bara fanns elva par gulärta, men det kanske aldrig funnit särskilt många.

Eftersom man noterat betestrycket för varje del-

område har man kunnat göra några analyser av hävdens betydelse. Trots att hävden anses vara en nyckelfaktor för strandängsfåglarna kan man inte visa på några riktigt tydliga resultat. Rödbenan har ungefär samma täthet från helt obetade till kraftigt betade områden. För tofsvipa får man en svagt positiv effekt men bara om man räknar med de ej alls hävdade områdena. En ganska måttlig hävd tycks alltså vara tillfylles. Men analysen av hävdens betydelse är naturligtvis högst preliminär. En närmare analys av det stora materialet, med hänsyn tagen till andra påverkande variabler, skulle vara av stort värde. Den väldiga variationen i tätheter oberoende av betestrycket tyder på att andra faktorer måste vara viktigare, eller i varje fall andra mått på hävden än de man registrerat. Den detaljerade redovisningen av primärmaterialet öppnar för fortsatta analyser som skulle kunna bli av stort värde för strandängsskötsel i allmänhet. Inte minst vore det värdefullt att få en analys av större sammanhängande områden och betydelsen den mosaik av olika hävdnivåer som finns inom sådana.

Länsstyrelsen för Gotland har nu ett utomordentligt fint underlag både för den framtida skötseln av strandängarna och för kontrollen av hur den framtida utvecklingen kommer att påverka fågelfaunan. Det omfattande fältarbetet utfördes av Tuomo Kolhmainen och Lars Tydén.

SÖREN SVENSSON

Mikael von Numers, 1995: **Distribution, numbers and ecological gradients of birds breeding on small islands in the Archipelago Sea, SW Finland.** *Acta Zoologica Fennica* No. 197, 127 sid. Finnish Zoological and Botanical Publishing Board, Helsinki. Pris: 225 FIM.

I denna avhandling om fågellivet i Skärgårdshavet introduceras ett nytt ord i det engelska språket: *fjärdicity*, d.v.s. fjärdighet i motsats till öighet, eller kanske riktigare tillbakaöversatt till svenska fjärdriktedom och örikedom. Skärgården indelas i olika zoner efter förhållandet mellan mängden öar och öppet vatten, fjärdar. Två av zonerna är den inre respektive yttre "fjärd-zone", d.v.s. den inre respektive yttre öfattiga zonen. Om det verkligen finns ett behov av att introducera detta ord kan diskuteras, men det illustrerar ändå det faktum att Östersjöns skärgårdar för många är en alldeles speciell naturtyp i ett internationellt sammanhang.

Skärgårdshavet, d.v.s. skärgården utanför sydväs-

tra Finland, är en av Östersjöns främsta pärlor, som väl tävlar med vilket annat skärgårdsområde som helst i Östersjön. Mikael von Numers har, till stor del tillsammans med Lars von Haartman, inventerat alla kobbar, skär och öar mindre än ca 4–5 ha inom ett 2700 kvadratkilometer stort område. Det har blivit inte mindre än 1641 stycken. Det gör denna undersökning till en av de absolut främsta som någonsin gjorts i Östersjön, ett arbete som ingen som sysslar med skärgårdarnas natur och fågelliv kan undvika att ta del av med hedern i behåll. Endast större öar som inte hyser några nämnvärda antal av sjöfåglar har lämnats oinventerade, vilket innebär att inventeringen är praktiskt taget fullständig med avseende på vattenfåglar, måsfåglar och vadare. För de öar som inventerats är den dessutom fullständig med avseende även på landfåglar.

Fältarbetet har utförts under nio år, 1982–1990. Inventeringsresultaten har redan tidigare använts i viss utsträckning för planering av naturvårdsåtgärder i området, men denna avhandling är den första samlade redogörelsen. Den inleds med allmänna beskrivningar av området, diskussion av inventerings- och bearbetningsmetoderna, sammanfattande diagram och tabeller över fåglarnas totala förekomst, klassificering av öarna i olika kategorier, samt indelning av skärgården i typiska zoner och fågelsamhällen. För detta används två ordinationsmetoder, DCA och PCA (korrespondens- resp. principalkomponentanalys). Totalt indelas skärgården i 28, av olika egenskaper präglade områden. Ett mindre område med 19 öar har använts som referensområde och inventerats samtliga år 1982–1991. För de flesta arter har det skett små förändringar, vilket innebär att tolkningarna av det totala materialet inte påverkats nämnvärt av förändringar under tiden, vilket är ett viktigt konstaterande eftersom olika delar av skärgården inventerats olika år.

En betydande del av avhandlingen består av artvisa redogörelser. Alla viktiga arter har egna utbredningskartor. Den i särklass vanligaste sjöfågeln var ejdern som med 7011 par fanns på 1191 öar, vilket innebar att den också var den vanligaste arten av samtliga. Bland sjöfåglarna var det sedan ett långt hopp ner till tvåan, som var silvertärnan med 3325 par. Därefter följde skrattnåsen (3490), fiskmåsen (1969), gråtrutten (1532), viggan (824), fisktärnan (748) och tobisgrisslan (667). Bland de sällsyntare kan nämnas labben med 57 par och skrântärnan med 41 par. Sällsyntast av alla var berganden med ett enda par i en fisktärnekoloni.

Bland vadarna var strandskatan talrikast (385 par jämt spridda på 367 öar i alla zoner). Näst vanligast

var roskarlen med 335 par, hyfsat väl spridda på 299 öar med klar tendens till de mest marint präglade områdena. Jag kan inte hitta något nämnt om denna arts historia, vilket hade varit intressant med tanke på att den tycks ha problem på flera håll i Östersjön. Förekomsten på de nitton referensöarna tyder dock inte på någon pågående nedgång i området. Roskarlen varierade mellan 2 och 6 par utan någon trend uppåt eller neråt.

Listan över landfåglar är lång men antalet par var mycket lågt för de flesta arter, vilket är naturligt med tanke på att de inventerade öarna var små och många utan eller med mycket litet skog. Allmänt var bofinken och sädesärulan med 1043 resp. 925 par. Bland de åtta vanligaste arterna var det av naturliga skäl arter som tillhör öppen mark som dominerade. Fem av dessa arter var sådana: sädesärula, stenskvätta, ärtsångare, skärpiplärka och törnsångare. Litet överraskande är kanske att ärtsångaren klassificeras som öppenmarksart, men så var faktiskt fallet. Den fjärde vanligaste landfågel var en karaktärsart på de skogfattiga men enbuskrika yttre öarna. På många småöar i det yttre havsbandet var ärtsångaren en dominant och bara i den allra yttersta zonen var törnsångaren vanligare än ärtsångaren. Den mest marina av landfågeln var skärpiplärkan med 232 par, nästan uteslutande på de helt obeskogade yttre skären.

Den avslutande diskussionen tar upp flera olika aspekter av en zoogeografisk analys såsom biotop-effekter och arealeffekter (för landfåglar). Ett kapitel ägnas den intressanta frågan om betydelsen av mås- och tärnkolonier för andra arter. Analyserna visar på flera sådana associationer: viggan attraheras till kolonier av såväl små måsfåglar som trutar, ejdern till trutkolonier, svärtan till silvertärnkolonier, strandskatan och roskarlen till kolonier av tärnor och små måsar, större strandpiparen till kolonier av silvertärna och fiskmåsar och rödbenan till kolonier av silvertärna. Riklig förekomst av tärnor och måsar har alltså starka positiva effekter på förekomsten av flera andra skärgårdsarter, och det är därför mycket bekymmersamt när tärnor och måsar minskar i antal.

Sammanfattningsvis är detta en utomordentligt värdefullt avhandling, baserat på ett synnerligen noggrant och omfattande fältarbete. Den borde kunna stimulera till liknande studier i övriga skärgårdssområden i Östersjön. Östersjöns skärgårdar utgör en naturtyp som, om än inte helt unik, utgör en av de mest särpräglade och värdefulla naturtyper som Östersjöns stater har att värda.

SÖREN SVENSSON

Peter Berthold, 1996: **Control of Bird Migration**. Chapman & Hall, London. 355 sid. Medlemspris i Naturbokhandeln:

Fågelflyttningens mysterier, ty den innehåller fortfarande många mysterier, omfattar samma kontraster mellan å ena sidan förutsägbarhet och å andra sidan flexibilitet och oväntade beteenden som allt annat i fåglarnas liv och uppträdande. Hur långt en liten sångare flyttar kan med stor precision förutsägas med hjälp bara två faktorer, nämligen antalet inskränningar på handpennornas fan och längden av carpometacarpus (de hos fåglarna sammansmälta benen i f.d. handled och fingrar). Hela 83 % av variationen i flyttlängd kan förklaras! Men å andra sidan ger den moderna ortieringsforskningen, både med orienteringstrattar och liknande instrument och med hjälp av radiosändare (bl.a. satellitföljningar), en mycket komplicerad bild av oförutsägbara rörelser, riktningar, etapper och rastupphåll. Trots flera decenniers sofistikerad forskning om fåglarnas orienteringsmekanismer, vet vi i dag inte säkert vilka nycklar fåglarna använder sig av under sina färder över hav och kontinenter. Det vi vet är att de hittar vägen!

Peter Bertholds gloria lyser främst genom de banbrytande insatser som han gjort när det gäller den inre styrningen av fåglarnas tidsschema under flyttningen och under senare år de studier av den genetiska grund som styr fåglarnas flyttlängd och flyttriktning. Studierna av fåglarnas tidsschema har huvudsakligen gjorts i laboratorier med tonvikt på fotoperiodiken, d.v.s. hur den relativa längden av dag och natt, eller frånvaro av växlingar mellan dag och natt, påverkar flyttaktiviteten under dygnet och året. De genetiska studierna har främst utförts på svarthättor. Fåglar med olika flyttvanor har korsats med varandra och Berthold har funnit att flyttvanorna är ärftliga eftersom de överförs till avkomman. Om svarthättor ur flyttande populationer korsas med sådana ur stationära populationer kommer en del av avkomman att flytta på ett sätt som ligger mellan föräldrarnas vanor. Det gäller både längd och riktning. Genom dessa experiment har Berthold visat att flyttvanorna mycket snabbt formas av det naturliga urvalet.

Den egna forskningens resultat får naturligtvis sin beskärda del av boken. Men boken är mycket mera än så. Den är en imponerande litteraturgenomgång och blir därför en suverän katalog över det som publicerats i ämnet. Referenslistan omfattar över 800 uppsatser. Boken består av två huvudavdelningar, en om de fysiologiska kontrollmekanismerna och

en om orienteringsmekanismerna. I ett tredje, kort kapitel behandlar Berthold flyttningens mikroevolution, bl.a. den under senare år snabba ökningen av övervintrande svarthättor i England från kontinentens häckningsområden. Orsaken till ökningen anses vara ökad födotillgång på grund av vintermatning vid fågelborden. De genetiska och evolutionära spekulationer som presenteras rörande fenomenet är dock fortfarande oklara. Svarthättefrågan är intressant ur svenska perspektiv också. Som framgått av en artikel i *Ornis Svecica* (vol. 4, 1994, sid. 105) har det skett en betydande ökning av övervintrande svarthättor i Sverige också. Det är intressant att spekulera i om det är svenska svarthättor, som normalt flyttar till tropikerna, som börjat övervintra, eller om det är fåglar från kontinenten som flyttar norrut för att övervintra i Sverige. Det senare förefaller nästan mest troligt!

Om man skall jämföra de två huvudkapitlen framstår det rätt klart att det är de endogena kontrollmekanismerna som är Bertholds kompetens- och huvudsakliga intresseområde. De behandlas på 200 sidor medan orienteringsmekanismerna behandlas på bara 25 sidor. I detta avseende är boken klart obalanserad, och det är inte meningsfullt för den som enbart är intresserad av orienteringsmekanismerna att köpa den. Däremot är det svårt att hitta en bättre och mera aktuell sammanfattning av forskningsläget och den befintliga litteraturen när det gäller det förstnämnda problemområdet.

Avslutningsvis kan det finnas skäl att se litet in i framtiden. När det gäller de endogena mekanismernas roll under experimentella situationer börjar kunskapen att bli mycket god, även om det är ett relativt litet antal arter som ännu är väl studerade. Här ligger den framtida forskningens viktigaste uppgift i att studera hur dessa genetiskt och hormonellt styrda system modifieras av omvärldsfaktorerna, sådana som fåglarna möter dem ute i verkligheten. Här kommer sannolikt mycket att hända inom de närmaste åren i och med att man successivt kommer att kunna identifiera genernas roll allt bättre och studera förekomsten och frånvaron av variation i specifika delar av arvsmassan. På orienteringssidan torde det allt överskuggande problemet vara att identifiera det organ eller det sätt på vilket fåglarna registrerar den information som ligger till grund för orienteringen, kanske främst hur de registrerar magnetfält, om det nu är de som används som primär orienteringsbas. Ett tredje område som lovar mycket för framtiden och som kommer att utvecklas explosionsartat är att med satelliter följa radiosändarförsedda fåglar. Precisionen är i dag så god att man med mycket högrums- och tidsupplösning kan registrera fåglarnas rörelser över hela jordklotet och följa deras flyttning i alla detaljer. Det är till och med möjligt att samtidigt registrera vissa fysiologiska tillstånd och aktiviteter. Här öppnas fantastiska perspektiv för studier av fågelflyttningen i både stort och smått och hela dess variationsrikedom.

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